Vol. 36. Parts 10–12. Pp. 133–176*. 58 figs. 15th, December 1961

THE PROCEEDINGS
OF THE
ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Series A

GENERAL ENTOMOLOGY

World List abbreviation : *Proc. R. ent. Soc. Lond.* (A)

CONTENTS

	PAGE
WYATT, I. J. Pupal paedogenesis in the CECIDOMYIIDAE (DIPTERA).—I	133–143, 14 figs.
SURTEES, GORDON. Spermathecal structure in some COLEOPTERA associated with stored products	144–152, 25 figs.
CLARIDGE, M. F. Biological observations on some eurytomid (Hymenoptera : Chalcidoidea) parasites associated with Compositae, and some taxonomic implications	153–158, 7 figs.
EVANS, M. E. G. The fronto-clypeal region and the stomodeum in COLEOPTERA . . .	159–162, 2 figs.
RAMCHANDRA RAO, Y. Notes on the life-history and habits of *Chonocephalus depressus* de Meijere (DIPTERA : PHORIDAE) in South India	163–167, 10 figs.
DYTE, C. E. and BLACKMAN, DOROTHY G. A pearl-eyed mutation in *Gnathocerus cornutus* (Fab.) (COLEOPTERA : TENEBRIONIDAE), with notes on similar variants in other beetles .	168–172
BOOK NOTICES	173
INDEX	174–177

LONDON
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 14s. 6d.

* With Title Page, Contents and Index

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded 1833. Incorporated by Royal Charter 1885

Patron:

HER MAJESTY THE QUEEN

OFFICERS AND COUNCIL FOR THE SESSION, 1961–1962

PROFESSOR G. C. VARLEY, *President*
MR. R. B. BENSON, *Vice-President*
DR. N. E. HICKIN, *Vice-President*
MR. M. J. WAY, *Vice-President*
DR. C. G. BUTLER, *Treasurer*
DR. PAUL FREEMAN, *Secretary*
MR. W. H. POTTS, *Editor*

Other Members of Council

PROFESSOR D. S. BERTRAM
DR. M. I. CRICHTON
DR. K. U. CLARKE
MR. R. G. DAVIES
DR. A. M. EASTON
DR. J. E. HARKER
DR. P. T. HASKELL
DR. B. R. LAURENCE
MR. H. OLDROYD
SIR BORIS UVAROV, K.C.M.G., F.R.S.

MISS E. EVANS, *Registrar*

Finance and House Committee

PROFESSOR D. S. BERTRAM (*Chairman*)

MR. J. P. DONCASTER
DR. J. A. FREEMAN, O.B.E.
DR. N. E. HICKIN
DR. D. J. LEWIS
MR. M. E. SOLOMON

Publication and Library Committee

MR. R. G. DAVIES (*Chairman*)

DR. J. D. CARTHY
DR. P. T. HASKELL
DR. C. G. JOHNSON
MR. D. LEATHERDALE
MR. G. E. J. NIXON

Conservation (Insect Preservation) Committee

MR. R. B. BENSON (*Chairman*)

DR. B. M. HOBBY
MR. T. G. HOWARTH
DR. A. M. MASSEE
MR. F. T. VALLINS
MR. M. J. WAY

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Dr. H. E. Hinton, F.R.S., appointed 1958.
2. **Local Committee of Management of Wicken Fen.**
   Dr. John Smart, appointed 1960.
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. N. D. Riley, C.B.E., appointed 1955.
4. **New Forest Association.**
   Mr. C. W. Mackworth-Praed, appointed 1948.
5. **New Forest Joint Committee.**
   Lt.-Col. F. C. Fraser, appointed 1949.
6. **Field Studies Council.**
   Dr. W. H. Thorpe, F.R.S., appointed 1944.
7. **Yorkshire Naturalists' Trust, Ltd.**
8. **The Biological Council.**
   Dr. N. E. Hickin, appointed 1952.
9. **The Parliamentary and Scientific Committee.**
   Dr. N. E. Hickin, appointed 1953.
10. **British Co-ordinating Committee for Nature Conservation**
    Mr. R. B. Benson, appointed 1960.
11. **Council for Nature.**
    Dr. N. E. Hickin, appointed 1958.

PUPAL PAEDOGENESIS IN THE CECIDOMYIIDAE (DIPTERA).—I

By I. J. Wyatt
(*Glasshouse Crops Research Institute, Littlehampton, Sussex*)

Introduction

The phenomenon of paedogenesis, or the production of young by immature insects, has been known for almost a century. At the time of its discovery by Wagner (1862), the concept was received with considerable scepticism and opposition, and although today it is generally accepted it is still regarded as a biological curiosity. Few instances of paedogenesis have been recorded and, apart from some dubious records of reproduction by pupae discussed below, all have concerned larval paedogenesis.

In the past, two claims have been put forward concerning paedogenesis in pupae, but neither has been substantiated. Firstly, Grimm (1870) described oviparous paedogenesis by the pupa of a chironomid. His interpretation of the process, however, was disputed in turn by Schneider (1885), Zavrel (1926) and Vandel (1931). Finally, Hinton (1946) pointed out that the eggs were laid by the fully formed adult, still within the pupal cuticle. This is readily seen in Grimm's original illustration. A second instance of pupal paedogenesis was reported by Klyver (1931), who claimed that an unidentified species of Cecidomyiidae exhibited the paedogenetic production of eggs and larvae by both mother larvae and pupae. The account was very brief and gave no details of the mechanism of reproduction. Pritchard (1960) has shown this gall-making midge to be *Dasyneura* sp. nr. *trifolii* Loew, and claims that it reproduces only by adult females. Thus both these early reports of pupal paedogenesis can be discounted.

Though these early claims have been disproved, two genuine instances of paedogenesis by pupae have recently come to light. Nikolei (1958) described an unusual paedogenetic process, in an undescribed cecidomyiid, in which a larva having a fully formed sternal spatula (usually characteristic of a final instar) moulted again before producing its young. He apparently failed to realise that the resulting stage had lost its sternal spatula, as well as other larval characters, and had acquired many attributes of the pupa. Preserved material was passed, for taxonomic study, to Möhn (1960), who recognised the reproductive stage as a form of pupa and termed it a " hemipupa ". He named the species *Tekomyia populi* Möhn. This new genus is allied to the paedogenetic genus *Mycophila* Felt.

In February, 1958 the author received a sample of mushroom compost from Mr. E. V. Henry of Padstow, Cornwall. This was infested with whitish cecidomyiid larvae, which superficially resembled those of *Heteropeza pygmaea* Winnertz, although on closer examination they proved to be distinct. The larvae fed on mushroom mycelium grown on malt agar slopes. A few pupated normally and produced imagines, which were subsequently described as a new genus and species, *Henria psalliotae* Wyatt (1959, 1961). Most larvae, however, moulted to an unusual elliptical form which, as in the case of *T. populi*, is perhaps best regarded as a pupal stage. This then produced, within its haemocoele, numerous embryos which later emerged through the cuticle as young larvae.

The following account describes the mode of reproduction and form of the hemipupa in more detail. As the species is potentially an economic pest and subject to confusion with other mushroom infesting species, the opportunity is taken to describe the larval instars.

METHODS

Larvae are readily reared in the laboratory by two methods, the first suitable for experimental purposes and short-term cultures, and the second more fitted to long-term maintenance of stocks and population studies. The methods are: (*a*) Mushroom mycelium is grown on sterile slopes of 2 per cent. malt agar for four days. Young larvae are then immersed for about a minute in 8 per cent. formaldehyde to sterilise the cuticle. The gut contents are apparently already sterile, for no contamination of the culture ensues. A single larva is then transferred by a fine camel-hair brush from the formaldehyde to a mushroom culture. The culture tube is then inverted (because wandering larvae tend to move upwards) and placed in a dark incubator at 75° F. In two to three weeks a new generation is produced, and, to ensure optimum conditions for growth, the young larvae are immediately transferred to fresh mushroom cultures. If larvae are left on a single culture for several generations, overcrowding and starvation result, and occasionally adults may be produced.

(*b*) Mushroom compost, as prepared for commercial mushroom growing, is washed and filled into " Kilner " jars after surplus water has been squeezed out. The glass lid is replaced by a disk of asbestos with a quarter-inch introduction hole at the centre, which is plugged with cotton wool. The jars are sterilised for two hours with steam at 20 lb./sq. in. On cooling, mushroom mycelium is inoculated and a week later sterilised larvae are introduced. This method is useful for maintaining stock cultures and, as the mycelium ages, a swarm of flies is frequently induced.

The study of larval skins has presented several difficulties owing to the impermeability of the cuticle and severe contraction on killing. The following method has, however, proved very satisfactory. A live larva is placed in water under a cover slip and gently pressed with a needle. The cuticle is thus fully distended; it ruptures near the head and all the body contents are squeezed out. While still under pressure the slide is gently heated to fix the body muscles. The skin is then removed to a clean slide and mounted in Faure's medium with the ventral surface uppermost. The preparation is very transparent but all structures can be readily seen with a phase contrast microscope.

THE PAEDOGENETIC CYCLE

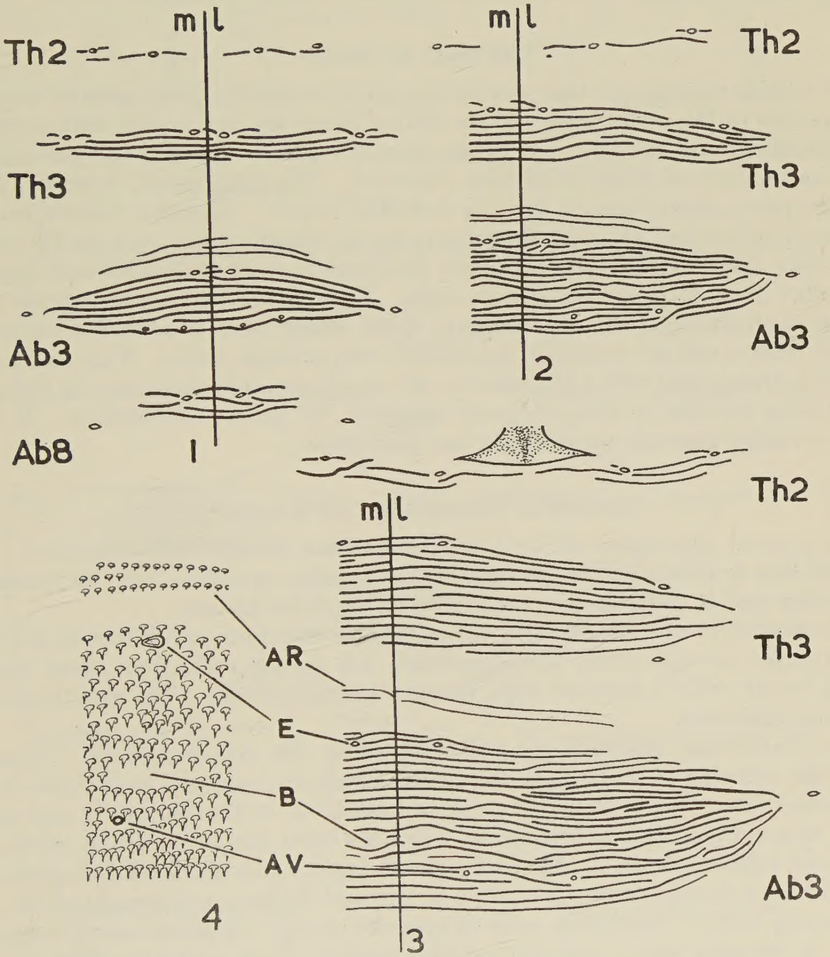
The following details are for larvae raised by method (*a*) above. Even with conditions standardised as far as possible, considerable variation occurs in the rate of growth of larvae, and consequently in the duration of a complete paedogenetic cycle.

The newly emerged larva is 0·8 mm. long and feeds on the youngest mushroom hyphae by puncturing the cell wall and sucking out the cell contents. Feeding may take place on, or below, the surface of the agar. The first instar has the two thoracic eye spots contiguous, no sternal spatula and no trace of imaginal disks. Moulting takes place on the third day when the larva is about 1·3 mm. long. Ecdysis is seldom observed and appears to cause only a brief cessation of feeding. Length of stadia can therefore only be determined by the examination of skins of known ages.

The second instar resembles the first, except in size, and continues feeding until it is about 2·3 mm. long. The second moult occurs when the larva is a week old.

The third and final larval instar is distinguished by the possession of a sternal spatula and separated eye-spots. This stage in other paedogenetic species is normally destined to pupate and produce an adult, and is therefore often referred to as the " imago-larva ", or by some authors as the " pupa-larva ". At first only the anterior prong of the sternal spatula is discernible, but it progressively darkens from the anterior end until it is entirely black at pupation. In this species the third instar may lead either to the paedogenetic or to the sexual cycle. In the former case the eye-spots are only slightly separated, the thorax tapers, imaginal disks are reduced and the cuticle remains smooth. In the latter instance eye-spots are widely separated, the thoracic segments with their imaginal disks are enlarged and the cuticle becomes transversely wrinkled.

At about twelve to fifteen days old the larva prepares to pupate, having grown to about 3·0 mm. It finds a suitable crevice in the agar or cavity under the mycelium, frequently alongside the original inoculum. Alternatively, it will excavate a chamber in the agar. Then it spins a flimsy cocoon in which it pupates, to form not a normal pupa but the unusually modified hemipupa which is described later.



Figs. 1–4.—*Henria psalliotae* Wyatt. Diagrams of spinule rows on thoracic and abdominal segments of larvae : (1) first instar ; (2) second instar ; (3) third instar ; (4) second instar, enlarged cross-section of third abdominal creeping welt. *Th*2, mesothorax ; *Th*3, metathorax ; *Ab*3, third abdominal segment ; *Ab*8, eighth abdominal segment ; *AR*, anterior spinule rows ; *AV*, anterior ventral papillae ; *B*, bare areas ; *E*, elliptical papillae ; *ml*, median line.

Considerable variation occurs in the time when the ovaries begin to develop. Embryos have been found in an early third instar larva, while on the other hand hemipupae have contained ovaries in initial stages of development. Normally the ovaries begin to proliferate and the embryos to break free into the haemocoele just before pupation. Within the hemipupa the embryos grow very rapidly and appear to undergo normal embryological development. The tissues of the hemipupa are absorbed, leaving little more than the tangled tracheal system within the mother cuticle. When fully formed the embryos are enclosed in three membranes, the serosa, the amnion and the embryonic cuticle. The latter thickens anteriorly just before emergence, to form what is presumably a hatching spine. The young larva breaks through the two outer membranes and then emerges from the embryonic cuticle, leaving the thickened process as a prominent bow-shaped structure within the body cavity of the mother. Larvae leave the mother by rupturing the cuticle, usually posteriorly. A hemipupa derived from a well-fed larva normally produces from 30 to 60 young, although as many as 96 and as few as 2 have been recorded.

The Sexual Forms

No reliable method has been devised as yet to induce the production of imagines. Thus details of the development of the sexual forms are not known with certainty. It is presumed that the first two instars closely resemble those of the paedogenetic cycle, as no distinct forms have been observed. The final instar, however, differs from the paedogenetic form in the way described above. Pupation follows the same sequence as described, although the pupa shows no abnormalities, and the fly emerges a few days later. Practically all adults produced have been females and these are able to lay about four parthenogenetic eggs. These hatch into normal larvae which resume paedogenesis. On one occasion three males were produced with several females from a culture originally inoculated with a single larva. This culture had become contaminated with a *Chaetomium* sp., so sex determination may be controlled by nutrition and not, as was previously imagined, by genetic constitution. It is not known whether bisexual reproduction can take place.

External Morphology of Larvae

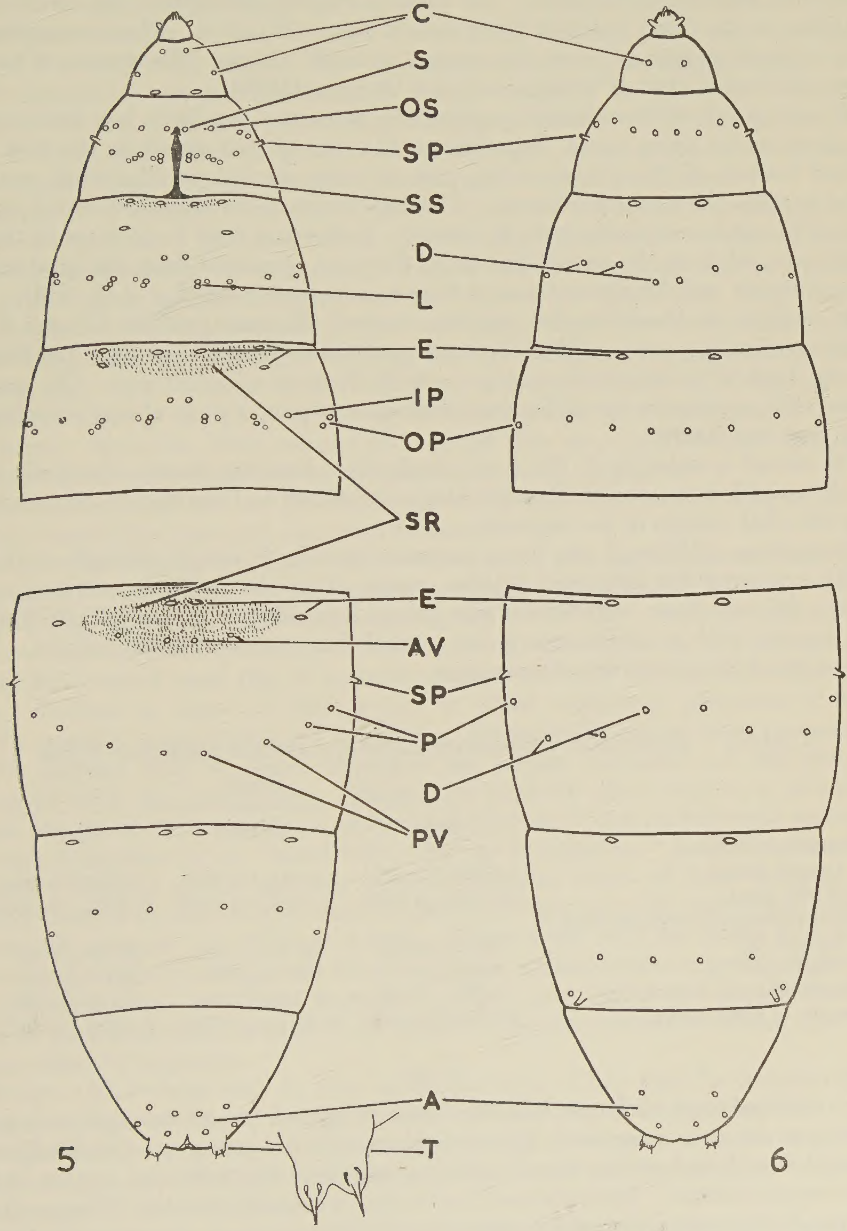
The general appearance of the larval instars has already been described. It is intended here to give a detailed account of the cuticular structures both for taxonomic comparison and to facilitate the separation of the three instars.

The Head is brown, conical and varies little in size from one instar to the next. The antennae are apparently one-segmented, and a little more than three times as long as broad, with a rounded apex bearing a small papilla. The mouthparts are small and indistinct.

The Thorax and Abdomen are yellowish-white, the cuticle smooth. A pair of prominent spiracles is present on the eighth abdominal segment in the first instar. The second instar bears, in addition, visible spiracles on the prothorax and on the second to seventh abdominal segments, while the third instar has a pair on the first abdominal segment as well. The anal segment bears a pair of short bifid appendages each with two strong spines. The anus is terminal without a protrusible tube.

Creeping welts.—Transverse rows of spinules occupy elliptical areas, commonly known as creeping welts, near the anterior margin of the ventral surface of many segments (figs. 1–4). The number and arrangement of these rows provides the most reliable method of distinguishing instars. Considerable anastomosis and variation of the rows, especially in the later instars, makes counting difficult, although an approximation is adequate to determine the instar.

No creeping welts are present on the collar segment, prothorax or anal segment (fig. 5). A single broken row of spinules is sometimes found on the mesothorax of the first instar, and one or two rows are usually present in the later instars (figs. 1–3, *Th.* 2). The metathorax bears five rows in the first instar, seven in the second and thirteen in the third (figs. 1–3, *Th.* 3). The first seven abdominal segments bear approximately 8, 15 and 22 rows in respective instars, though rather less on the two anterior segments (figs. 1–3, *Ab* 3). The second and third instars are also distinguished from the first by a series of 8 bare areas (see figs. 3–4, *B*) across the posterior half of the abdominal creeping welts. These do not seem to represent papillae, as has been suggested by some authors (*e.g.* Hennig, 1948). The first instar may also have about three short spinule rows on the eighth abdominal segment (fig. 1, *Ab*8), but these are sometimes absent and are never represented in later instars. Slightly



Figs. 5–6.—*Henria psalliotae* Wyatt. Diagrams of papilla arrangement on thoracic and seventh (typical) to ninth abdominal segments of third instar larva (for clarity all papillae are shown approximately six times the scale of the outline) : (5) ventral view ; (6) dorsal view. *A*, anal papillae ; *AV*, anterior ventral papillae ; *C*, collar papillae ; *D*, dorsal papillae ; *E*, elliptical papillae ; *IP*, inner pleural papillae ; *L*, lateral papillae ; *OP*, outer pleural papillae ; *OS*, outer sternal papillae ; *P*, pleural papillae ; *PV*, posterior ventral papillae ; *S*, sternal papillae ; *SP*, spiracle ; *SR*, spinule rows ; *SS*, sternal spatula ; *T*, terminal papillae.

anterior to the abdominal creeping welts are a few isolated spinule rows: usually one on the two anterior abdominal segments and two on subsequent segments (figs. 3–4, *AR*).

Papillae in these larvae are reduced to minute subcuticular rings, above which the cuticle is barely raised. Consequently their disposition becomes more difficult to ascertain the earlier the instar. To avoid a lengthy description the arrangement of papillae in the third instar is illustrated in figures 5 and 6. The arrangement in earlier instars appears to be similar, except as noted above. The system of nomenclature adopted is that of Rübsaamen and Hedicke (1926).

Of each group of three lateral papillae (*L*), the outer papilla is less distinct than the others in the third instar, indistinct in the second and absent in the first. An unusual feature of the species is the pair of outer sternal papillae (*OS*) near the sternal papillae (*S*) on the prothorax. The disposition of the anterior ventral papillae (*AV*) on the abdomen varies with the instar: in the first they lie in front of the last spinule row, while in the second and third they are separated from the hind margin of the creeping welt by about three or four rows respectively (figs. 1–3, *Ab*3).

In addition to these circular papillae, several elliptical papillae (*E*) are found. In this species they are considerably more prominent than the circular papillae and take the form of a tongue-like process arising from an elliptical rim. The pair at, or near, the posterior edge of the metathoracic creeping welt is absent or indistinct in the first two instars.

The sternal spatula (fig. 5, *SS*) has a single blunt anterior prong; the shaft, when fully developed, is somewhat dilated in the anterior half and has two broad extensions along the hind margin of the segment.

Dimensions.—Although the larva increases steadily in length throughout its life, the dimensions of the distended cuticles, prepared by the method described earlier (p. 134), fall into three well-defined size groups according to instar. Table I shows mean figures, with standard errors, for several dimensions of such cuticles. Each mean is based on at least ten observations.

TABLE I.—*Dimensions from larval cuticles of* Henria psalliotae *Wyatt*

	Instar		
	First	Second	Third
Distended cuticle—			
Length (mm.)	1·020±0·038	1·813±0·048	2·359±0·036
Width (mm.)	0·1500±0·0065	0·2846±0·0099	0·3624±0·0083
Third abdominal creeping welt—			
Length (μ)	19·12±0·65	36·16±1·22	56·50±1·40
Width (μ)	96·6±4·7	183·5±7·2	235·3±5·6
Length of head capsule (μ) .	2·956±0·097	3·718±1·27	3·412±0·093
Length of antenna (μ) . .	0·6522±0·0133	0·6915±0·0097	0·7684±0·0221

PUPA

The external form of the pupa is illustrated in figure 7 but no description is given, except in so far as it is necessary for comparison with the hemipupa described below. The head is as broad as the thorax and bears, behind the antennae, a pair of long slender cephalic setae. The cuticle of the thorax is entirely smooth. The prothorax bears two long prothoracic horns or spiracles, which have about eight pairs of elliptical openings along the outer edge towards the apex (fig. 10). The legs show the full adult segmentation and the wings, which fold around the legs, possess terminal appendices to accommodate the long fringing hairs of the wing of the adult. The abdomen is covered with short, irregularly arranged spinules, except on a median region of the anal segment and areas along the posterior ventral margin of each segment. Spiracles are evident on the fifth, sixth and seventh abdominal segments and are small conical structures with a single subterminal aperture (fig. 11). Pupae are about 1·4 mm. long and vary little in size.

HEMIPUPA

The paedogenetic form of the pupa (fig. 8) differs considerably from a normal pupa. It is elliptical in shape and three to four times as long as broad. Twelve segments are usually visible, the first three being thoracic and occupying only a sixth of the total body length. The anal segment forms a rectangular plate on the eighth abdominal segment and bears an ovoid vestige of the genitalia. The body cuticle is covered with short, irregularly arranged spinules resembling those of the pupa in form and distribution but, unlike the pupa, they extend over the entire thorax apart from a small anterior ventral region of the prothorax.

Spiracles.—Prominent features of the hemipupa are the prothoracic and posterior abdominal spiracles. The prothoracic spiracles (fig. 12) resemble a reduced form of the prothoracic horns of the true pupa, being one-third of the length and having about four pores. They project from the anterior edge of the prothorax. The posterior spiracles are similar in form and project posteriorly from the dorsal surface of the eighth abdominal segment (fig. 14); they are not found in the true pupa. Smaller spiracles (fig. 13) are visible on the fifth, sixth and seventh abdominal segments but differ from those of the pupa in having an anterior foot-like extension and three or four pores. Spiracles, often reduced to a simple tube or pore, also occur irregularly on one or both sides of the second to fourth abdominal segments.

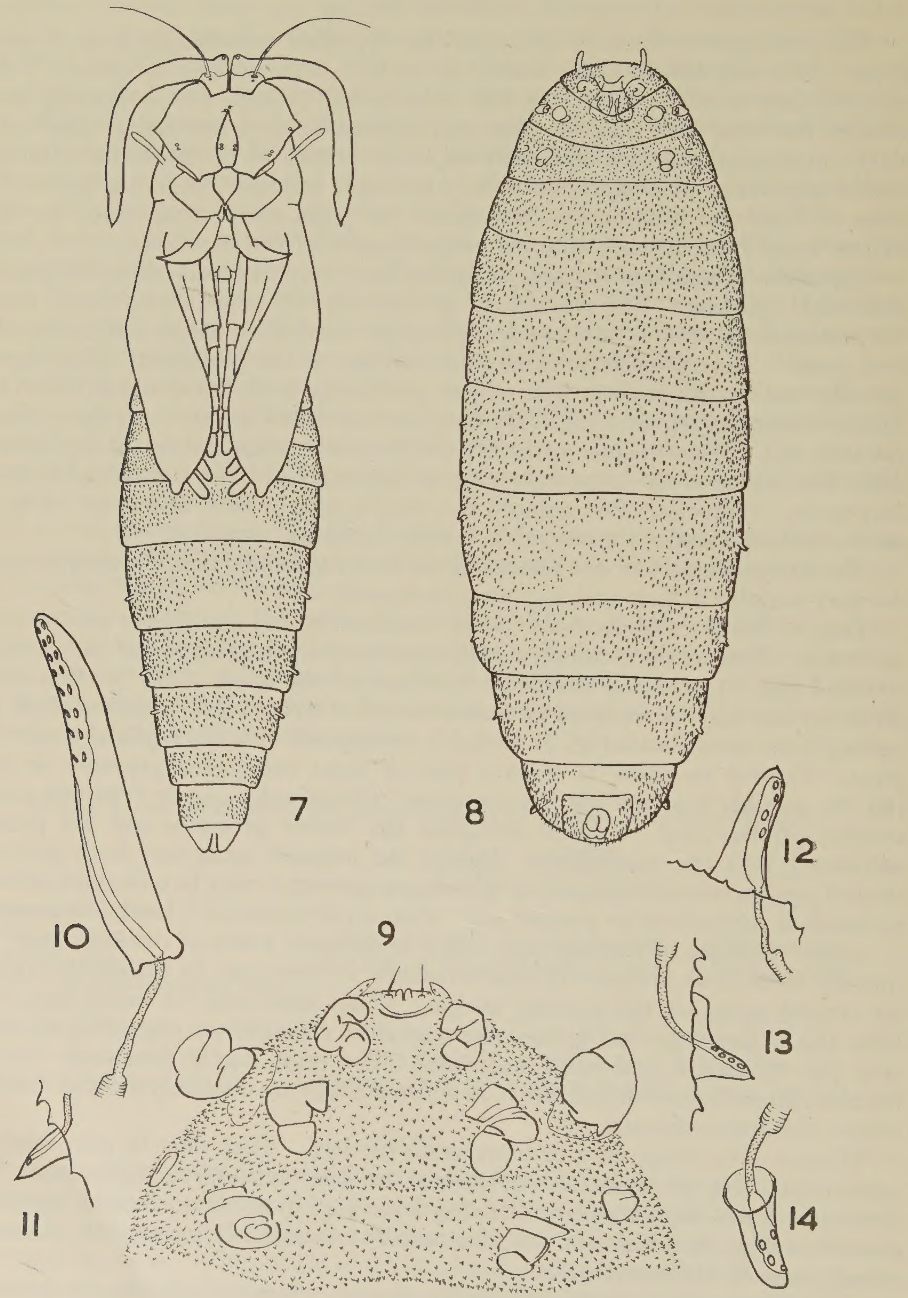
The above characters are present in all hemipupae but the following structures are very variable in form and may even be absent.

Head.—The form of the head varies considerably and homologies are difficult to ascertain. Frequently a complex pyriform cuticular invagination of the prothorax is found (fig. 8), which is presumed to represent the head. This is often absent, however, and may be replaced by various external structures. A pair of short setae arising from raised bases (fig. 9) probably correspond with the cephalic setae of the pupa. Ventral to these is often a pair of blunt contiguous processes or ridges (fig. 9), possibly representing the antennae. Occasionally one or even two pairs of smaller papillae may be found alongside the former processes and are probably associated with the mouthparts. Behind the cephalic setae may be a prominent conical process covered with strong spinules, suggesting it may be a thoracic structure, although it appears to be present only when an invaginated " head " is absent.

Legs.—Vestiges of the legs may occur in different states of development. Frequently there is no evidence of their existence, or they may be represented only by six smooth areas on the thoracic cuticle. These areas may be raised into simple lobes (fig. 8, first segment) or the lobes may show constrictions suggesting segmentation (fig. 8, second and third segments). The most highly developed condition found so far is illustrated in figure 9, in which the legs are distinctly divided into three or four distorted segments.

Wings.—The wings vary in form as do the legs. They may be completely unrepresented, but are more usually present as dark cuticular invaginations. More developed forms have simple protruding lobes (fig. 8) or more complex convoluted structures (fig. 9). Halteres are also usually represented by smooth, sometimes raised, areas on the metathorax.

Size.—Hemipupae vary considerably in size. This is undoubtedly associated with the state of nutrition during larval development. The number of young is, in turn, proportional to the size of the hemipupa : there is a linear relationship between number of young and volume. Thus the smallest hemipupa recorded produced two young and was 0·9 mm. × 0·28 mm. (flattened) ; a poorly-fed larva might give rise to a hemipupa 1·5 mm. × 0·54 mm., with 16 young ; a well-fed larva might produce a hemipupa 1·8 mm. × 0·68 mm. with 40 young, while the largest hemipupa measured



Figs. 7–14.—*Henria psalliotae* Wyatt: (7) normal pupal exuvium; (8) hemipupa, showing invaginated head and small vestigial appendages; (9) thorax of more highly-developed hemipupa, showing also cephalic setae and antennal vestiges; (10) prothoracic horn of pupa; (11) abdominal spiracle of pupa; (12) prothoracic spiracle of hemipupa; (13) abdominal spiracle of hemipupa; (14) posterior abdominal spiracle of hemipupa.

was 2·6 mm. × 0·74 mm. and gave birth to 71 young. The state of development of the head and appendages is not closely associated with size, nor is the condition of the head related to that of legs. In general, however, the development of legs and wings are correlated.

DISCUSSION

Two instances of pupal paedogenesis in Cecidomyiidae have recently been discovered, simultaneously and independently. The account by Möhn (1960) appeared only a month before a reference to the phenomenon by the present author (Wyatt, 1960). The two species involved, *Tekomyia populi* and *Henria psalliotae* are not closely allied, and, according to the latest revision of the group (Pritchard, 1960), would be placed in the separate subfamilies Lestremiinae and Cecidomyiinae respectively. Despite this, the paedogenetic stages of these two species are remarkably similar. In both, the cuticular structures of the larva, such as sternal spatula, creeping welts and small conical head with sucking mouthparts, are missing. On the other hand, they possess a spinulose cuticle, wing and leg vestiges, prothoracic spiracles and, in the case of *T. populi*, terminal papillae more typical of the pupa. In both, the embryos begin haemocoelous development in the final larval instar of the parent, which undergoes a moult to produce the unusual stage from which the young emerge. It may be concluded, therefore, that the final stages in both species are homologous both in form and function.

In the two earlier claims, discussed in the introduction, that the pupae of certain insects were able to reproduce paedogenetically, it has been shown that the interpretation was erroneous. In one species it is clear that the reproductive stage was the pharate adult and not the pupa. Is it possible that this might also be so with the recent discoveries ? There are two important differences. Firstly, there is no indication that an adult cuticle, or any internal structures, have been formed within the pupa ; in fact the reproductive stage, although possessing certain cuticular characters peculiar to the pupa, shows a great reduction in the structures destined to enclose adult appendages. Secondly, the method of reproduction, namely the haemocoelous production of many young, differs fundamentally from the normal adult process of laying a few eggs through the oviducts. It seems most unlikely, therefore, that reproduction in these instances is in fact by a pharate adult.

It is necessary to turn to larval paedogenesis to find a mode of reproduction comparable with that of *H. psalliotae* and *T. populi*. In doing so, we find that both species have close allies exhibiting larval paedogenesis, namely the genera *Leptosyna* Kieffer and *Mycophila* Felt respectively. Reproduction can take place in any larval instar of the known paedogenetic species. For instance, *Heteropeza pygmaea* Winnertz completes its whole paedogenetic cycle in the first larval instar ; in *M. speyeri* Barnes the ovaries begin proliferation soon after birth, but the young are not released until the second instar. If a larva is destined to become an adult and, on reaching the final instar, is placed on its own and provided with abundant food, its ovaries develop prematurely and young are produced by the normal paedogenetic method. This can occur both in *H. pygmaea* (Harris, 1925) and, in the author's experience, in *M. speyeri*. From the statement of Nikolei (1958), that " the mother is still able to crawl about while the first progeny are being shed " and that the mother has a sternal spatula, it might be concluded that *T. populi* can also produce at least some young before pupation. It is only necessary to take this sequence one step further to reach the condition normally found in *H. psalliotae* and *T. populi* : should a final instar larva, with haemocoelous embryos, undergo pupation, a paedogenetic pupa would be produced. This condition has not been induced in any other species and it should be pointed out that in *H. psalliotae* the process is normal even under wide variations in nutrition. Thus it appears to result from a genetically determined sequence, not from a rare " reversal of function " due to a sudden change in environment.

There may be some doubt whether the hemipupa truly represents the pupal stage, for superficially it resembles a larva more closely than a pupa. This resemblance is occasionally enhanced by the close adherence of the larval exuvium, with its sternal spatula, to the hemipupa, a fact which may have misled Nikolei. More detailed examination leaves little doubt, however, that the hemipupa is a form of pupa. The hemipupa occurs in the same relative position as the pupa in the life cycle. Thus a larva, having a sternal spatula typical of a final instar, prepares for pupation in the normal way but moults to the hemipupa instead of a pupa. The spinulose cuticle of the hemipupa closely resembles that of the pupa, though extending over the thorax. It is quite unlike the smooth cuticle of the larva, which bears regular spinule rows on the creeping welts. The possession, by some individuals, of vestigial thoracic appendages suggests that the hemipupa is a post-larval stage, although Hinton, in a private communication, has suggested that they may merely be everted imaginal disks. The hemipupa differs most markedly from the true pupa in the vestigial nature of these structures, and in the form of the head, yet the possession of thoracic appendages is possibly enough to distinguish the stage as a pupa rather than a larva. These cephalic and thoracic structures, when present, presumably represent degrees of suppression of the normal pupal appendages.

Spiracles are well developed in the hemipupa of *H. psalliotae* and resemble reduced forms of the prothoracic horns of the normal pupa. The abdominal spiracles are more elaborate than those of the pupa, yet their distribution more closely resembles that of the second instar larva. Thus spiracles are seen on all segments from the second to the eighth abdominal, the latter being the most prominent. The spiracles of the larva, however, are simple and tubular. Similarly, in *T. populi*, the prothoracic spiracles of the hemipupa are sieve-like, as in the normal pupa.

The larvae of all Cecidomyiidae possess a small conical head with minute but complex mouthparts. However, in the hemipupa of *H. psalliotae*, the head is not readily discernable and the mouthparts, if apparent, are simple lobes more closely resembling the reduced condition of the adult. Only the antennal vestiges, when present, might be said to resemble those of the larva more than the adult. Therefore there is little evidence that this reproductive stage represents a larva, while most supports the assumption, made originally by Möhn, that it is an aborted pupa.

To conclude, the larva of either *H. psalliotae* or *T. populi* undergoes a normal life cycle until reaching the third and final larval instar. It may then moult to a normal pupa, which finally produces an adult fly, or more usually the ovaries proliferate and haemocoelous embryos are produced. This " self-parasitism ", as it might be termed, has a profound effect on the formation of the pupa which is produced at the ensuing moult. All characters peculiar to the pupa, such as spinulose cuticle, multipored spiracles and a pair of cephalic setae, are retained. However, all structures normally destined to enclose appendages of the adult (the legs, wings, halteres, head capsule, antennae and mouthparts) are reduced to distorted vestiges or are absent entirely. It is from the integument of this malformed pupa that the family of young larvae finally emerges to repeat the paedogenetic cycle.

ACKNOWLEDGMENTS

I wish to thank Dr. H. E. Hinton of the University of Bristol for useful suggestions concerning interpretation of the facts.

REFERENCES

GRIMM, O. VON, 1870, Die ungeschlechtliche Fortpflanzung einer *Chironomus*. *Mem. Acad. Sci. St. Petersb.* **15** : 1–24. [English translation, *Ann. Mag. nat. Hist.* (4) **8** : 31–45 ; 106–15.]

HARRIS, R. G., 1925, Reversal of function in a species of *Oligarces*. *Biol. Bull.* **48**: 139–44.

HENNIG, W., 1948, *Die Larvenformen der Dipteren*, **1**. Berlin.

HINTON, H. E., 1946, Concealed phases in the metamorphosis of insects. *Nature, Lond.* **157** : 552–3.

KLYVER, F. D., 1931, Preliminary note on paedogenesis in a Cecidomyiid. *Pan-Pacif. Ent.* **8** : 9–10.

MÖHN, E., 1960, Studien an paedogenetischen Gallmückenarten (Diptera, Itonididae) I. *Stuttgarter Beiträge zur Naturkunde* **31** : 1–11.

NIKOLEI, E., 1958, Untersuchungen über den Generationswechsel pädogenetischer Gallmücken. *Rev. suisse. Zool.* **65** : 390–6.

PRITCHARD, A. E., 1960, A new classification of the paedogenetic gall midges formerly assigned to the subfamily Heteropezinae (Diptera : Cecidomyiidae). *Ann. ent. Soc. Amer.* **53** : 305–16.

RÜBSAAMEN, E. H. and HEDICKE, H., 1926–39, Die Cecidomyiden und ihr Cecidien. *Zoologica, Stuttgart* **29** : 1–350.

SCHNEIDER, A., 1885, *Chironomus grimmii* und seine Parthenogenesis. *Zool. Beitr., Berl.* **1** : 301–2.

VANDEL, A., 1931, La parthenogenese. *Encycl. sci.* : 140–2.

WAGNER, N., 1862, Parthenogenesis in the larva of insects [*in Russian*]. *Sci. Mem. Kasan Univ.* **1** : 25–111.

WYATT, I. J., 1959, A new genus and species of Cecidomyiidae (Diptera) infesting mushrooms. *Proc. R. ent. Soc. Lond.* **28** : 175–9.

—— 1960, A talk about cecids. *Mushr. Gr. Assn. Bull.* **122** : 55–56.

—— 1961, The male of *Henria psalliotae* Wyatt (Diptera : Cecidomyiidae). *Proc. R. ent. Soc. Lond.* **30** : 1–3.

ZAVŘEL, J., 1926, *Tanytarsus connectens*. *Publ. Fac. Sci. Univ. Masaryk* **65** : 1–47.

SPERMATHECAL STRUCTURE IN SOME COLEOPTERA ASSOCIATED WITH STORED PRODUCTS

By Gordon Surtees

(*Agricultural Research Council, Pest Infestation Laboratory, Slough, Bucks.*)

The site of sperm storage in female insects, the spermatheca or receptaculum seminis, is primarily an invagination of the integument at the posterior end of the venter of the eighth abdominal segment. Typically there is a duct, which may be expanded to form a copulatory bursa, leading from the vagina to the spermathecal chamber. A tubular gland associated with the latter structure may also be present. A study of the present type serves mainly as an addition to our knowledge of the internal structure of Coleoptera associated with stored products and in a number of cases is of taxonomic and phylogenetic significance. Furthermore, in population studies, such data aid the assessment of the proportion of females fertilised and therefore of those contributing to population growth, a point of considerable importance when density is excessively low or tending to decline because of control measures.

The general arrangement indicated above is variously modified and some of the major features common to groups of families are as follows. A well-marked, more or less strengthened bursa copulatrix is found in the Dermestidae, Anobiidae, Anthribidae, Cucujidae, Cleridae, Bruchidae and Nitidulidae (fig. 1*a*) whilst in the Ostomatidae, Ptinidae, Curculionidae, Silvanidae and Bostrichidae it is reduced or absent. In the Tenebrionidae the bursa varies in size and in some species is almost absent (fig. 1*b*), whilst in *Alphitophagus bifasciatus* Say, *Lasioderma serricorne* F., *Stegobium paniceum* L., *Araecerus fasciculatus* Deg. and the *Dermestes* species it is a separate structure not directly connected to the spermathecal duct (fig. 1*c*). In most species the spermathecal chamber is well chitinised (fig. 1*d*) but in the Ptinids it is tubular (fig. 1*e*) and in some Silvanids consists of a number of small tightly packed tubules (fig. 1*f*), whilst in the Tenebrionids and Dermestids all of these types of structure occur. In some Ptinids, Silvanids and *Latheticus oryzae* Waterh. the gland referred to above is absent. Motile spermatozoa may be detected in most fertilised females without opening the spermathecal chamber.

The order in which the families are discussed is an arbitrary one, those primarily associated with grain and grain products being considered first, then those found on other products and finally those which feed on break-down products, waste materials or non-food substances.

Materials and Methods

All species examined during this study were taken from routine laboratory cultures. Freshly etherised adults were placed on a depression slide in normal saline and sufficient pressure applied to the abdomen with forceps to cause extrusion of the genitalia which were then grasped by a second pair so that the whole reproductive system could be drawn out. The muscles, tracheae and fatty material were cleared away from the vagina and bursa so that the spermatheca and duct could be located. Up to this point dissection was carried out under ×17·5 magnification but detailed examination was done under ×70 or more.

Species Examined

To facilitate reference to individual species in the following text a full list, with authorities, is given below.

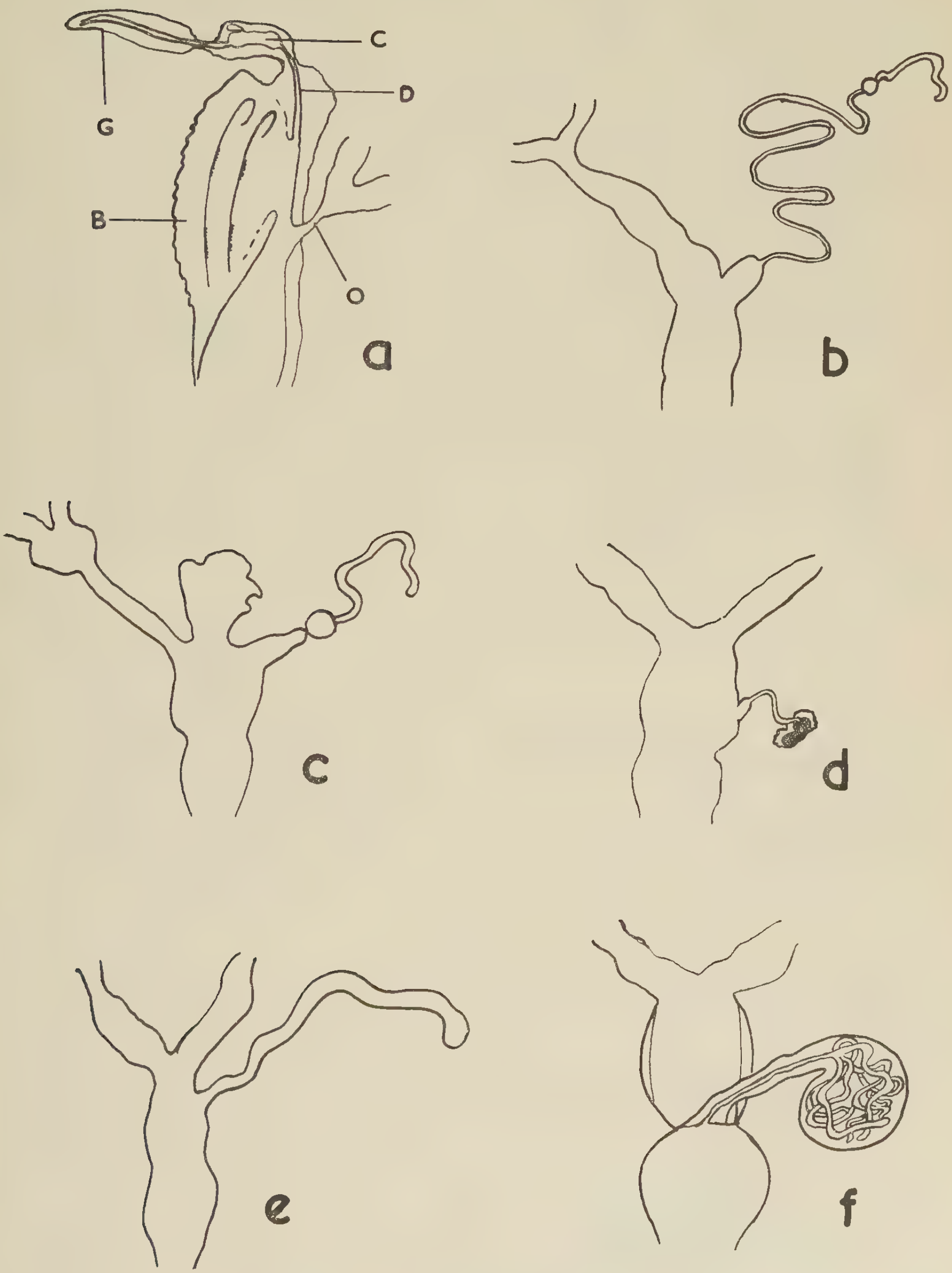


FIG. 1.—Some major modifications in female reproductive systems associated with the spermathecae (all × 17·5) : (*a*) strengthened bursa of *Trogoderma granarium* ; (*b*) reduced bursa of *Gnathocerus maxillosus* ; (*c*) bursa of *Alphitophagus bifasciatus* ; (*d*) chitinised storage chamber of *Sitophilus granarius*; (*e*) tubular storage region of *Ptinus sexpunctatus*; (*f*) storage region consisting of group of convoluted tubules in *Oryzaephilus surinamensis*. *B*, bursa ; *C*, spermathecal chamber ; *D*, duct ; *O*, common oviduct ; *G*, gland.

TENEBRIONIDAE

Tenebrio molitor L.
T. obscurus F.
Tribolium castaneum (Herbst)
T. madens Hint.
T. confusum Duv.
T. destructor Uytt.
T. anaphe Hint.
Gnathocerus cornutus (F.)
G. maxillosus (F.)
Alphitobius diaperinus (Panz.)
A. laevigatus (F.)
Alphitophagus bifasciatus (Say)
Palorus subdepressus Woll.
P. ratzeburgi (Wissm.)
Latheticus oryzae Waterh.

SILVANIDAE

Oryzaephilus mercator (Fauv.)
O. surinamensis (L.)
Cathartus quadricollis Guer.
Ahasverus advena (Waltl.)

CURCULIONIDAE

Sitophilus granarius (L.)
S. oryzae (L.)

CUCUJIDAE

Cryptolestes ugandae Steel and Howe
C. turcicus (Grouv.)
C. ferrugineus (Steph.)
C. pusillus (Schönherr)
C. pusilloides Steel and Howe
C. capensis (Waltl.)

BOSTRICHIDAE

Rhizopertha dominica (F.)

BRUCHIDAE

Callosobruchus chinensis (L.)
C. rhodesianus Pic
C. analis (F.)
C. maculatus (F.)
Zabrotes subfasciatus (Boh.)
Acanthoscelides obtectus (Say)
Caryedon gonagra (F.)

ANTHRIBIDAE

Araecerus fasciculatus (Deg.)

CLERIDAE

Necrobia rufipes (Deg.)

NITIDULIDAE

Carpophilus dimidiatus (F.)
C. hemipterus (L.)

ANOBIIDAE

Lasioderma serricorne (F.)
Stegobium paniceum (L.)

OSTOMATIDAE

Tenebroides mauritanicus (L.)

DERMESTIDAE

Dermestes lardarius L.
D. maculatus Deg.
D. haemorrhoidalis Kust and Praze
D. frischii Kug.
Trogoderma granarium Everts
T. inclusum (Creutz.)
T. anthrenoides (Sharp)
T. parabile (Beale)
T. glabrum Herbst

PTINIDAE

Ptinus hirtellus Sturm
P. pusillus (Sturm)
P. sexpunctatus Panz.
P. tectus Boield.
Trigonogenius globulus Sol.
Pseudeurostus hilleri (Reitt.).
Gibbium psylloides (Czemp.)
Tipnus unicolor P. and M.
Stethomezium squamosum Hint.
Mezium affine Boield.

TENEBRIONIDAE

Two main types of spermathecal structure are found in this family, one consisting of a group of sperm-storing ducts contained within a membrane and the other a single, more or less chitinised chamber. The former is seen in the two species of *Tenebrio*, *Tribolium castaneum* and *T. madens* and the latter, variously modified, in the remaining species of the family, with the exception of *Palorus ratzeburgi*, *P. subdepressus* and *Latheticus oryzae*, which have a structure similar to that found in the Ptinidae.

In *Tenebrio molitor* and *T. obscurus* the small, unstrengthened bursa terminates in a group of four convoluted ducts invested in a tough elastic membrane. These ducts contain motile spermatozoa in fertilised females. Arising subterminally from one side of the bursa is a narrow glandular region which has large-celled walls and a restricted lumen. A similar arrangement is found in *Tribolium castaneum* and *T. madens* where the gland has a chitinised base which appears to be closely associated with the common, distal ends of the sperm-storing ducts (fig. 2).

The more common type of arrangement found in Tenebrionids consists of a duct of varying length, leading from a more or less reduced bursa to a chitinised chamber and elongate gland. In *T. confusum*, *T. destructor* and *T. anaphe* the bursa is short and wide, terminating in a narrower region which divides into two branches, of which one enters the S-shaped chitinised chamber and the other the glandular region (fig. 3). The chamber is narrow at the duct entrance but more expanded distally whilst the gland is short in the first species and longer in the other two. In all three species motile spermatozoa can be detected easily within the chamber. In *Gnathocerus cornutus* and *G. maxillosus* the bursa is a short dilation to one side of the vagina leading in the former species directly to the spermathecal chamber, but giving rise in the latter to a long, much convoluted, spermathecal duct. In both species the chamber is transparent in unfertilised females but dark brown when containing spermatozoa. The entrance of the duct is marked by a flattened collar and at the opposite end of the chamber there is a finger-like projection, small in *G. maxillosus* (fig. 4) and large in *G. cornutus*, which appears to be associated with the gland. This latter structure is similar to that found in the *Tenebrio* species. In both species motile spermatozoa tend to aggregate in the region of the duct entrance and their movement can be observed inside the unbroken chamber. In *Alphitobius laevigatus* and *A. diaperinus* (fig. 5) there is little specific difference in spermathecal structure. The bursa is as wide as that in *Tenebrio*, terminating in a short, narrow, bifurcating duct, one branch of which leads to the chitinised chamber and the other to the long narrow gland. The chamber is an inverted, irregular U-shape with the duct entering the concave side. Motile spermatozoa are found in all parts. In *Alphitophagus bifasciatus* a short, wide duct leads directly from the vagina into a strongly chitinised chamber similar in structure to that of *Gnathocerus* (fig. 6). Between the spermathecal duct and common oviduct there is an irregularly shaped saccular region, which may be copulatory in function. The chitinised spermathecal chambers in the above species are approximately 0·1 mm. across and in *Tribolium castaneum* and *T. madens* the convoluted storage ducts within their investing membrane are approximately 0·15 to 0·20 mm. in diameter.

The structure in *Palorus ratzeburgi* (fig. 7) and *P. subdepressus* is similar, a short, wide copulatory region leading to a more muscular bursa. This gives rise to a weakly chitinised chamber some 0·3 mm. in length, which has transverse rings of strengthening. This latter region is dark brown in fertilised females but spermatozoa can only be seen when the chamber is broken. In *L. oryzae* a wide vagina divides terminally to produce a common oviduct and an elongate, muscular bursa which also serves as a sperm storage organ. As with the previous species, spermatozoa can only be seen when liberated.

SILVANIDAE

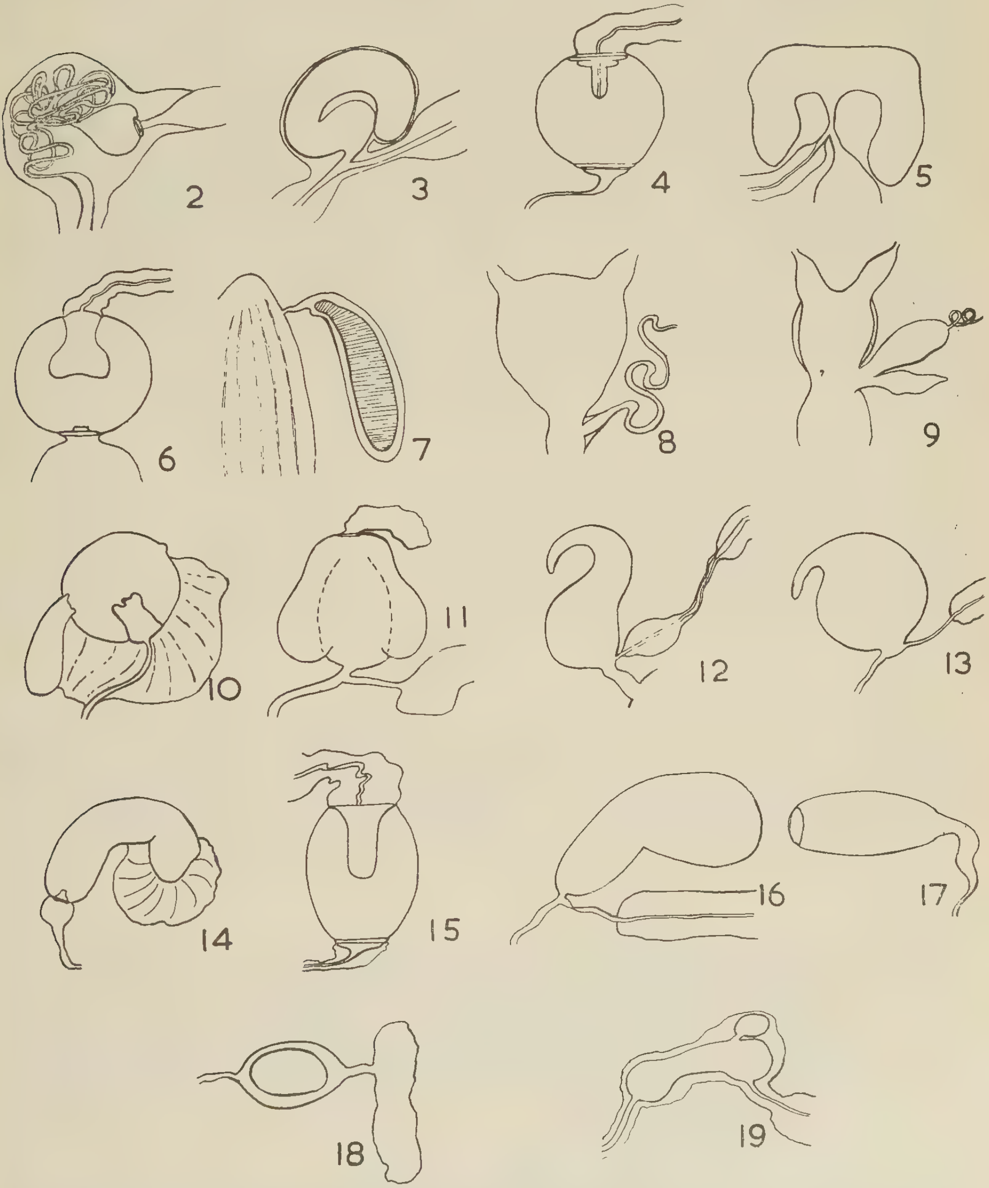
In *Oryzaephilus mercator* and *O. surinamensis* the upper part of the vagina gives rise to a wide common oviduct with thick muscular walls and a narrower duct with a restricted lumen which terminates in a group of densely packed tubes contained within a membranous chamber less than 0·1 mm. in diameter. The presence of motile spermatozoa is difficult to detect in this latter region unless it is pierced or broken. In *Cathartus quadricollis* (fig. 8) the spermathecal region is a simple convoluted duct arising from one side of the common oviduct and in *Ahasverus advena* (fig. 9) it consists of a larger and smaller chamber connected basally. In none of these species was any glandular region observed.

CURCULIONIDAE

No major differences were observed in the spermathecae of *Sitophilus granarius* and *S. oryzae*. In both, a short duct runs from a distended region of the vagina to the larger end of a comma-shaped chamber. Motile spermatozoa can be seen in all parts of this and intimately associated with it but without any apparent connection is a diffuse glandular region.

CUCUJIDAE

In *Cryptolestes ugandae*, *C. turcicus*, *C. ferrugineus*, *C. pusillus*, *C. pusilloides* and *C. capensis* there is marked uniformity of spermathecal structure, major specific differences occurring only in the chitinised skeletal elements of the bursa. This latter structure is approximately 0·3 mm. in length, whilst the chamber is less than 0·05 mm. in diameter. A short duct connects the bursa to the spherical, well-chitinised chamber which has a bulbular extension almost opposite to the duct entrance (fig. 10). Motile spermatozoa can be seen in all parts of the chamber. The gland is a diffuse mass of cells connected to the chamber in the region of the duct entrance.



Figs. 2–19.—A series of spermathecal chambers (dimensions as in text) : (2) *Tribolium castaneum* ; (3) *T. confusum* ; (4) *Gnathocerus maxillosus* ; (5) *Alphitobius diaperinus* ; (6) *Alphitophagus bifasciatus* ; (7) *Palorus ratzeburgi* ; (8) *Cathartus quadricollis* ; (9) *Ahasverus advena* ; (10) *Cryptolestes capensis*; (11) *Rhizopertha dominica*; (12) *Callosobruchus maculatus*; (13) *Caryedon gonagra* ; (14) *Araecerus fasciculatus*; (15) *Necrobia rufipes* ; (16) *Carpophilus dimidiatus* ; (17) *Lasioderma serricorne* ; (18) *Tenebroides mauritanicus*; (19) *Trogoderma granarium.*

BOSTRICHIDAE

No distinct bursa is seen in *Rhizopertha dominica*, the spermathecal duct arising from a slight dilation on one side of the common oviduct. This duct is short and divides into two branches, one entering the chamber and the other the elongate gland. The spermathecal chamber appears as a tightly convoluted, three-lobed chamber approximately 0·1 mm. in diameter (fig. 11) in all parts of which motile spermatozoa can be seen. From a point opposite to the entrance of the duct arises what is apparently a smaller glandular region.

BRUCHIDAE

As with the Cucujidae, few differences are found in the structure of the spermathecae, the major specific characters being associated with the large muscular bursa which is 0·4–0·5 mm. long. In all cases the short spermathecal duct runs from the side of the bursa to the chamber, giving off a small side branch to the typically elongate gland. In *Callosobruchus chinensis*, *C. rhodesianus*, *C. analis*, *C. maculatus* (fig. 12) *Zabrotes subfasciatus* and *Acanthoscelides obtectus* the chamber is a chitinised body some 0·15–0·20 mm. long, shaped like an inverted comma with the duct entering the lower end. In *Caryedon gonagra* the chamber is more circular, with a reduced upper arm (fig. 13). Motile spermatozoa may be seen in all parts of the chamber and in *Callosobruchus analis* and *A. obtectus* the upper part of the bursa has been seen to be distended with an opaque viscous mass in which, however, no motility could be observed.

ANTHRIBIDAE

The vagina of *Araecerus fasciculatus* gives rise to a muscular bursa, a common oviduct and a spermathecal duct. The latter is the shortest of the three and leads to a kidney-shaped chamber approximately 0·1 mm. long, transparent in unfertilised females but opaque in fertilised ones (fig. 14). Motile spermatozoa cannot be seen until the chamber is broken. The gland is a compact mass of cells closely associated with the chamber.

CLERIDAE

Necrobia rufipes has a muscular bursa, from the lower part of which arises a short spermathecal duct. This enters the lower end of a heavily chitinised, barrel-shaped chamber some 0·15–0·20 mm. long, opaque in both unfertilised and fertilised females (fig. 15). From the upper end of the chamber arises an elongate gland with an internal structure similar to that found in *Gnathocerus cornutus*.

NITIDULIDAE

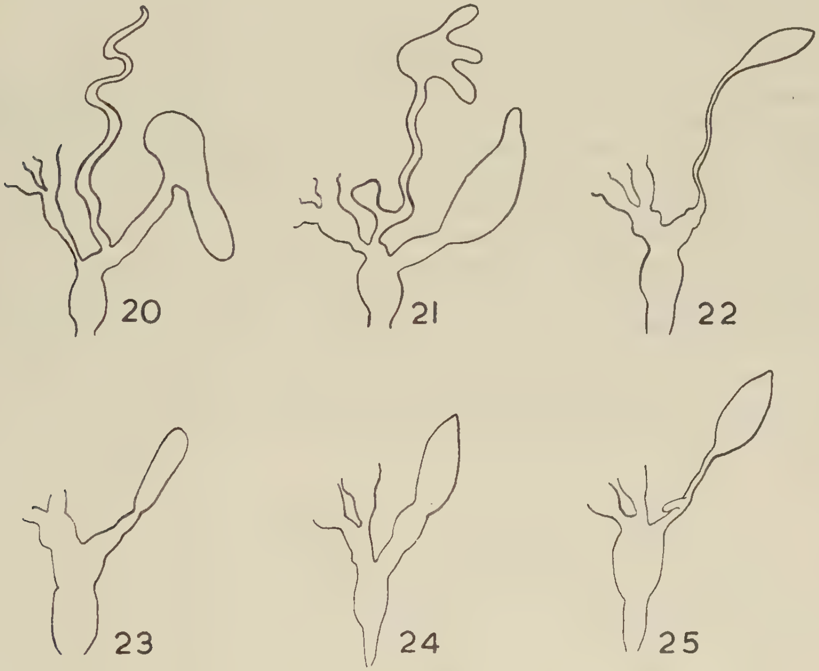
In both *Carpophilus hemipterus* and *C. dimidiatus* (fig. 16) the spermathecal chamber is connected to an irregularly shaped bursa by a short duct. This divides at the entrance to the chamber, to give a branch leading to the gland. In both species the chamber is irregularly shaped, approximately 0·15 mm. long and slightly reflexed about its mid-point. In fertilised specimens motile spermatozoa can be seen in all parts of the unbroken chamber.

ANOBIIDAE

The major feature of the female reproductive system in *Lasioderma serricorne* is its extreme muscularity. The vagina gives rise to a large, bulbous bursa, a common oviduct and a spermathecal duct which runs the length of the bursa before dividing into two branches. One of these leads to the ovoid chamber, 0·1 mm. long (fig 17), which is transparent in unfertilised females but darker in fertilised ones. The second branch of the duct leads to an elongate gland. In *Stegobium paniceum* the system is less muscular, the irregularly-shaped bursa connects to the vagina by a narrow neck and the gland is more diffuse.

Ostomatidae

Tenebroides mauritanicus has a reduced bursa lying to one side of the common oviduct. The spermathecal duct runs from this to one end of an ovoid chamber in which spermatozoa are found centrally (fig. 18). From the opposite end a short duct leads to a narrow, tubular gland.



Figs. 20–25.—Tubular spermathecal systems: (20) *Dermestes lardarius*; (21) *D. frischii*; (22) *Ptinus pusillus*; (23) *Trigonogenius globulus*; (24) *Gibbium psylloides*; (25) *Mezium affine.*

Dermestidae

In all of the *Dermestes* species examined, *D. lardarius* (fig. 20), *D. maculatus*, *D. haemorrhoidalis* and *D. frischii* (fig. 21), the vagina gives rise to a common oviduct, a long narrow spermathecal duct and a large muscular bursa. In the first two of these species the lower region of the duct serves as a sperm storage organ, there being no further differentiation into chamber or gland. In the latter two species there is a basal dilation to one side of the duct, which serves as a storage chamber, and terminally there is an irregularly-shaped gland. In *Trogoderma parabile*, *T. inclusum*, *T. granarium* (fig. 19), *T. glabrum* and *T. anthrenoides*, the main specific differences occur in the skeletal elements of the large bursa. The chamber is lateral to the bursa in *T. anthrenoides* but terminal to it in the remaining species. In all cases the spermathecal duct is short and wide, and leads to a large, elongate chamber with circular bands of strengthening joined by a shorter connecting duct to a small, round chamber approximately 0·1 mm. in diameter. The gland arises from the larger of the two chambers.

PTINIDAE

In all the ptinid species examined, the spermathecal arrangement consists of a simple duct without noticeable differentiation into chamber or gland. In *Ptinus sexpunctatus* and *P. pusillus* (fig. 22) there is a wide, loosely convoluted duct which is expanded slightly distally. Spermatozoa can only be seen in the basal region. In *Trigonogenius globulus* (fig. 23) the distal region is more expanded and longitudinal muscular elements are discernable. In *Pseudeurostus hilleri*, *Gibbium psylloides* (fig. 24), *Tipnus unicolor* and *Stethomezium squamosum* the arrangement is similar, with spermatozoa located basally but with a more distinct expansion of the terminal half and in *Mezium affine* (fig. 25) there is a marked lateral dilatation basally which contains spermatozoa.

SUMMARY

The spermathecal system found in the Coleoptera of stored products is described and figured here ; typically, it consists of a duct running from the vagina to the storage chamber, associated with which is a tubular gland. A bursa copulatrix may be present, directly or indirectly connected to the spermathecal duct. This system is variously modified in a number of families. A bursa with skeletal elements is found in some Dermestidae, and Anobiidae, the Anthribidae, Cucujidae, Cleridae and Bruchidae whilst it is reduced or absent in the Ostomatidae, Ptinidae, Curculionidae, Silvanidae, Bostrichidae and some species of the Tenebrionidae. Most species have a well-chitinised storage chamber but the Ptinidae have a tubular one, in the Silvanidae it consists of a group of small tubules and in the Tenebrionidae and Dermestidae all three types are found. The gland is found variously modified in all species except in the Silvanidae, Ptinidae and *Latheticus oryzae* (Tenebrionidae). All the figures and descriptions were taken from freshly etherised and dissected adults

BIOLOGICAL OBSERVATIONS ON SOME EURYTOMID (HYMENOPTERA: CHALCIDOIDEA) PARASITES ASSOCIATED WITH COMPOSITAE, AND SOME TAXONOMIC IMPLICATIONS

By M. F. Claridge
(Department of Zoology, University College, Cardiff)

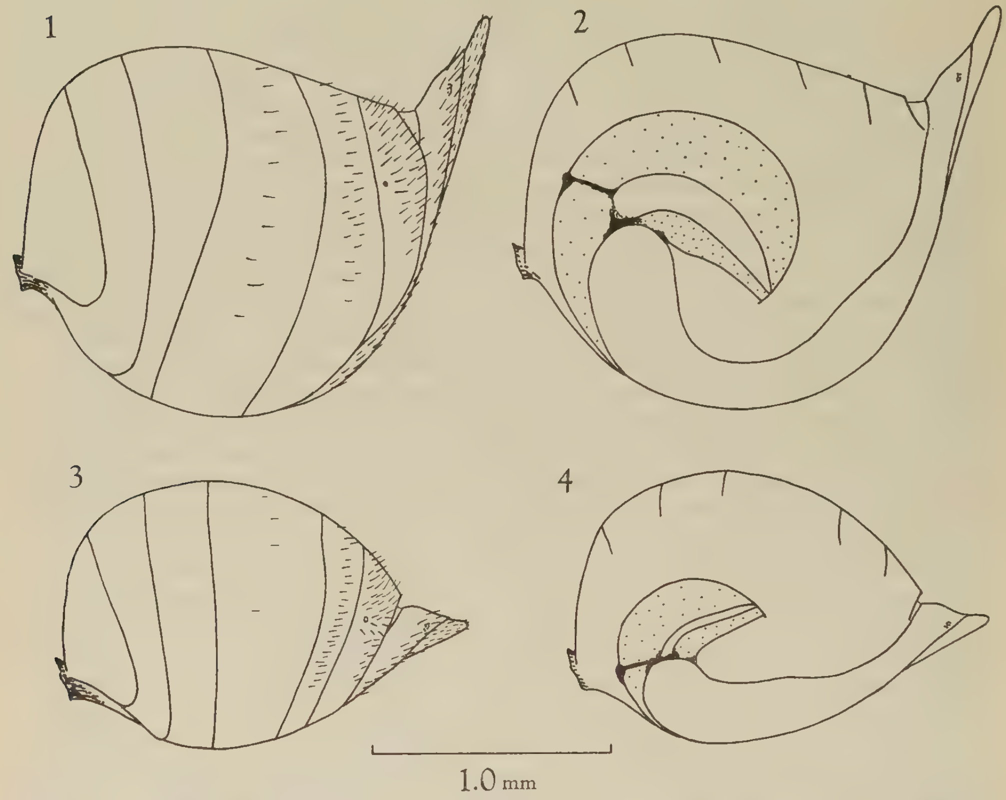
Naturalists for many years have collected plant galls and reared from them large and miscellaneous collections of insects, including many parasitic Hymenoptera. As early as the end of the eighteenth century, Fabricius (1798) described his *Ichneumon serratulae* (now in the genus *Eurytoma*) from specimens reared from galls on stems of *Serratula arvensis* L. (now in the genus *Cirsium*), the common creeping thistle. Some of the most popular plants with such workers have been the various Composite species, which are attacked by a wide variety of gall-forming insects. Although much rearing work has been carried out, it has usually been limited to collecting the parts of the plants concerned at a suitable season and awaiting the emergence of the insects. In this way a large collection can be obtained, but little is learnt of the true habits of the species concerned. The interrelationships of hosts and parasites are uncertain and the separation of phytophagous from entomophagous forms may be very difficult. Furthermore, collecting often tends to be indiscriminate so that mixed collections of galls may be kept unwittingly and any resulting host records will be doubtful. With little extra labour the same original plant material could be made to yield detailed information on such matters. If the galls, stems, or whatever the plant material may be, are opened at a stage when the larvae within are fully fed (this will often be the whole period of the winter months), they can be removed together with cast skins, egg-shells, host remains, *etc.*, and isolated in small gelatin capsules. Here they will usually pupate and emerge successfully. In this way can be built up a fairly detailed picture of the life histories concerned. Such methods were first effectively employed by Varley (1947) in his work on the parasites of the knapweed gall-fly, *Urophora jaceana* (Hering). I have used similar techniques with a wide diversity of gall- and stem-living insects and it is the purpose of this paper to describe the interrelationships of four species of *Eurytoma* which parasitise gall-formers on various Composites in Britain, and to discuss briefly some of the taxonomic implications of such studies.

None of the names here used for *Eurytoma* species will be found in Kloet and Hincks (1945).

Eurytoma serratulae (Fab.) (= *E. tristis* Mayr (Claridge, 1960, *Ent. Medd.* **29** : 249))

E. serratulae has been recorded from galls of the trypetid fly, *Urophora cardui* (L.), usually under the name of *E. tristis* Mayr, *e.g.* Mayr (1878) and Niblett (1956). *U. cardui* forms the common spindle-shaped galls on stems of *Cirsium arvense.* The gall consists of a series of vertical larval chambers surrounding the stem axis (fig. 6). Adult females of *E. serratulae* oviposit within the early instar host larvae during the summer, when the galls are only partly formed. The parasite larvae develop internally whilst the hosts feed and grow within the developing gall. Normal unparasitised larvae overwinter in a fully-fed condition. However, those attacked by *E. serratulae* appear to pupate in the late summer : that is, a puparium is formed. If such a puparium is opened, it is always found to contain a final instar larva of the *Eurytoma*, and no true pupa of the host is formed. This phenomenon, usually inaccurately termed premature pupation, is widespread amongst internal parasites of dipterous larvae. The subject has been discussed by Varley and Butler (1933), and Niblett (1956) has noted it for *E. serratulae.* The appearance of an opened gall with a fully fed larva and parasitised puparium is shown in figure 6.

E. serratulae seems to be a specific parasite of *U. cardui*, at least in Britain. Rivosecchi (1958) has recorded *E. tristis* from *Tephritis stictica* Loew in Italy. However, Dr. Rivosecchi has sent me some of his specimens and they are certainly not *E. serratulae* (= *E. tristis*). Unfortunately, the identity of his interesting species is at present uncertain.



Figs. 1–4.—Female gasters in lateral view. External view of (1) *Eurytoma tibialis* ; (3) *E. serratulae.* Diagrammatic dissections to show ninth tergite and ovipositor of (2) *E. tibialis* ; (4) *E. serratulae.*

Eurytoma tibialis Boh. (= *E. curta* auctt., *nec.* Walk.)

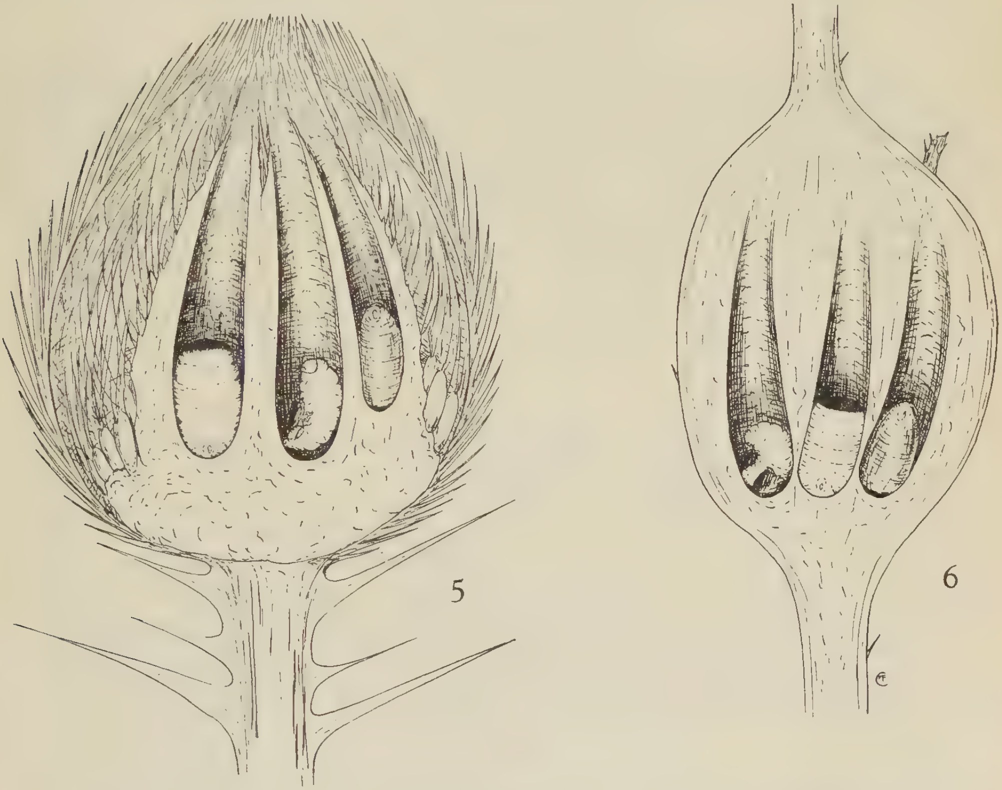
E. tibialis (usually wrongly called *E. curta*) is very closely allied to *E. serratulae*, but differs clearly in the shape of the female gaster (figs. 1, 3). The difference in shape can be seen to be due to the extension and curvature of the ninth tergite of *E. tibialis*, associated with its longer ovipositor (figs. 2, 4).

A wide variety of trypetid species are attacked, but all have in common the habit of forming larval galls within the flower heads of their host plants. The detailed biology of *E. tibialis*, as a parasite of *Urophora jaceana* (Hering) in the heads of the lesser knapweed, *Centaurea nigra* L., has been studied by Varley (1947). I have reared it as a parasite of *Urophora stylata* (Fab.) in heads of the spear thistle, *Cirsium vulgare* (Savi) Ten., and have also seen bred material from *U. solstitialis* (L.) in the musk thistle, *Carduus nutans* L., and *U. cuspidata* (Meigen) in the greater knapweed, *Centaurea scabiosa* L. Numerous records have been published of nongall-forming hosts, but I have been unable to confirm them by means of the abovementioned critical rearing techniques. It seems likely that the species is definitely restricted to trypetid species forming flower-head galls.

The life history is very similar to that of *E. serratulae.* Oviposition is within the early instar host larvae and apparent premature pupation of parasitised larvae takes place (fig. 5).

Eurytoma robusta Mayr

Superficially, adult *E. robusta* resemble *E. tibialis*, particularly in the distinctive shape of the female gaster, which is almost identical in the two species (fig. 1). In fact, they are best placed in different species groups within the genus. *E. robusta* and its allies possess, in front of the mid coxae, a distinctive mesosternal shelf, which is bounded anteriorly by a well-developed ridge. In *E. tibialis* and *E. serratulae* the mesepisternum slopes almost directly down to a small tooth in front of each mid coxa.



FIGS. 5–6.—Vertical sections through overwintering trypetid galls : (5) *Urophora stylata* in head of *Cirsium vulgare*, showing trypetid larva, larva of *Eurytoma robusta* with host remains, and puparium parasitised by *Eurytoma tibialis* ; (6) *Urophora cardui* in stem of *Cirsium arvense*, showing trypetid larva, larva of *E. robusta*, and puparium parasitised by *E. serratulae*. (Not to scale.)

Host records for *E. robusta* show that it attacks a wide variety of trypetid galls. Varley (1937) has given detailed biological information on it as a parasite of *Urophora jaceana* (Her.). I have reared specimens from larvae taken from galls of *U. stylata*, *U. jaceana* and *U. cardui*, and have seen series bred from galls of *U. solstitialis* and *U. cuspidata.* Thus it appears to attack the complete range of hosts of *E. tibialis* and also that of *E. serratulae.* However, the larval habits are quite different from either of these species.

Adult females of *E. robusta* normally oviposit later in the season than the other two species, when the host larvae are relatively larger. The egg is deposited either on the body of the larva or simply in the cell itself. Immediately after hatching, the parasite larva attacks its much larger host. It grows rapidly, completely devouring the trypetid, and itself overwinters as a fully-fed larva. Thus, when a gall is opened in the winter, the parasite, together with remains of the *Urophora* and its own egg shell, are found (figs. 5, 6). This is quite unlike those cells attacked by either of the other two species which at this stage would be within the host puparium. The interrelationships of these three species are summarised in figure 7.

Eurytoma strigifrons Thomson

E. strigifrons resembles *E. robusta*, but differs in its slightly shorter ovipositor and differently shaped mesosternal shelf. In Britain *E. strigifrons* is parasitic in galls of the cynipid, *Isocolus rogenhoferi* Wachtl, in flower heads of the greater knapweed, *Centaurea scabiosa* L. The galls of this species are situated on the inner surfaces of flower bracts and are normally unilocular. The life history is very similar to that of *E. robusta.* The eggs are laid within the host larval cell and the parasite is ectophagous. Both eggs and larvae are very like those of *E. robusta*, which have been described by Varley (1937).

There are no previous reliable host records for this species, which may often be confused with *E. robusta.* It is probably a specific parasite of *I. rogenhoferi.*

Discussion

The four species whose life histories have been described briefly above are related ecologically by their similar host preferences (fig. 7). It has been shown that the closely allied species, *Eurytoma serratulae* and *E. tibialis*, though attacking allied hosts, have no actual overlap in their host ranges. Biologically, the hosts differ in at least one obvious respect : that of *E. serratulae* forms galls on stems, whilst those of *E. tibialis* are flower-gall formers. Both parasite species attack the gallicolous larvae at an early stage, when the galls are only beginning to form. Adult males of the two species are exceedingly difficult to separate morphologically. Females are easily separated by differences in gaster shape, which, it is suggested, are functionally correlated with differences in ovipositor length. The latter in turn can be correlated with host preferences. The longer ovipositor of *E. tibialis* would be necessary for probing in through a flower head, whilst the shorter one of *E. serratulae* has only to reach larvae within a developing stem-gall. Thus, it seems reasonable to associate the obvious taxonomic differences with the host preferences of the two species.

From a general consideration of the differences between sympatric species, that is, species whose breeding ranges and seasons overlap in nature (*see* Cain, 1953), it is clear that they may be of at least two types, defined by the different selective pressures producing them. Firstly, there are those differences which are associated with the genetic isolating mechanisms—*e.g.* markings or structures used in specific courtship or recognition displays, none of which have been demonstrated definitely in the *Eurytoma* species under discussion. Secondly, there are those features associated with ecological differences which tend to reduce or eliminate interspecific competition. The gaster shapes correlated with length of ovipositor in *E. tibialis* and *E. serratulae* seem to be examples of the latter type.

Since *E. tibialis* and *E. serratulae* are truly sympatric, at least over part of Britain, it is of interest to speculate on the nature of the isolating mechanisms operating between them. Though the latter are not known, some factors can certainly be eliminated. By the very fact that the species are sympatric there can be no mechanism involving temporal isolation. The ecological and associated morphological differences, discussed above, also probably have little relevance in this respect, since it seems that they are independent of factors involving the maintenance of genetic isolation, the essential criterion for specific distinction (*see* Claridge, 1960). This is supported by the widespread occurrence of sibling species, which, though genetically isolated, show only very slight morphological differences. The true isolating mechanisms in this example may possibly be found in differences of courtship behaviour associated with physiological differences. From this it can be argued that the genetic isolation of the two species would not be affected if their gasters were similar. Indeed, if their hosts, though including no species attacked by both, all formed similar galls, it is likely that they would have similar gasters. They would then be extreme siblings and probably would not be recognised in orthodox taxonomy. Thus, forms with wide host ranges should be studied very critically, since they may in reality consist of groups of extreme siblings. Of course it is not suggested that all polyphagous species are in fact species aggregates, but the need for careful biological studies on all species is clearly demonstrated.

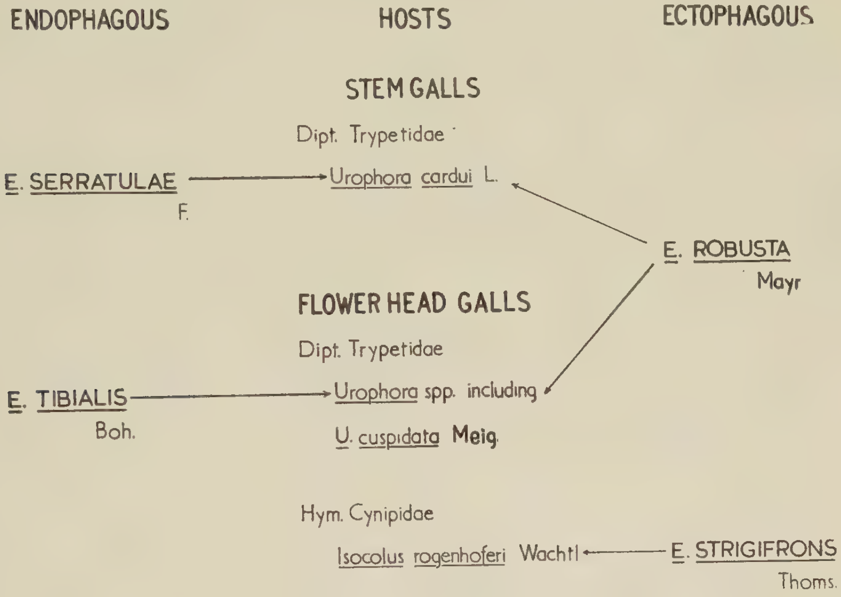


Fig. 7.—Summary of host interrelationships of four *Eurytoma* species.

The second pair of closely allied species described above, *E. robusta* and *E. strigifrons*, are less easily separated with dead adult material. *E. robusta* has been shown to attack not only trypetid flower-head galls, potential hosts of *E. tibialis*, but also stem-galls of *U. cardui*, potential hosts of *E. serratulae*. It is worth noting that the female gaster closely parallels that of *E. tibialis*, correlated similarly with a long ovipositor. An interesting problem associated with *E. robusta* is the difference in searching behaviour which must exist between it and the two more specific parasites of the same hosts. Unfortunately, no comparative data are available on this topic and it is useless to speculate at present. *E. strigifrons* differs from the other three species in that its host is a cynipid. However, the latter is a flower-gall former, attacking *Centaurea scabiosa*. The same flower head may also be attacked by the trypetid, *Urophora cuspidata*, which in turn may be parasitised by both *E.*

tibialis and *E. robusta.* Therefore a single head may yield all three species! *E. strigifrons* and *E. robusta* are similar enough to be confused, if details of their ecological separation were unknown. Thus it is obvious that, at least in certain groups of Chalcidoidea, life history and similar studies are not only of general interest in themselves but may be essential techniques of the taxonomist as well as the ecologist.

ACKNOWLEDGMENTS

I wish to thank Dr. B. W. Staddon, who has spent much time discussing the theoretical background to this paper. I thank also Professor G. C. Varley, Hope Department of Entomology, Oxford, in whose department much of the rearing work was carried out, for his many helpful suggestions, and Professor J. Brough for reading the manuscript.

REFERENCES

CAIN, A. J., 1953, Geography, ecology and coexistence in relation to the biological definition of the species. *Evolution* **7** : 76–83.

CLARIDGE, M. F., 1960, The biospecies in entomology. *Nature, Lond.* **188** : 1172–3.

FABRICIUS, J. C., 1798, *Supplementum Entomologiae Systematicae.* Hafniae.

KLOET, G. S. and HINCKS, W. D., 1945, *A check list of British Insects.* Stockport.

MAYR, G., 1878, Arten der Chalcidier-Gattung *Eurytoma* durch Zucht erhalten. *Verh. zool.-bot. Ges. Wien* **28** : 297–334.

NIBLETT, M., 1956, Some Dipterous inhabitants of thistles. *Ent. Rec.* **68** : 75–78.

RIVOSECCHI, L., 1958, Note sui parassiti dei Tripetidi, I. *Eurytoma tristis* Mayr e *Ormyrus hungaricus* Erdös (Hymenoptera Chalcididae). *Boll. Zool. agr. Bachic., Milano* **1** : 187–208.

VARLEY, G. C., 1937, Descriptions of the eggs and larvae of four species of Chalcidoid Hymenoptera parasitic on the Knapweed Gall-fly. *Proc. R. ent. Soc. Lond.* (B) **6** : 122–130.

—— 1947, The natural control of population balance in the Knapweed Gall-fly (*Urophora jaceana*). *J. anim. Ecol.* **16** : 139–187.

VARLEY, G. C. and BUTLER, C. G., 1933, The acceleration of development of insects by parasitism. *Parasitology* **25** : 263–8.

THE FRONTO-CLYPEAL REGION AND THE STOMODEUM IN COLEOPTERA

By M. E. G. Evans
(*Zoology Department, University of Manchester*)

In the insect embryo, the frontal ganglion is derived from the dorsal wall of the stomodeum just within the mouth, and receives connections from the tritocerebrum. Snodgrass (1935, 1947) used this relationship to mark the position of the true mouth in post-embryonic stages. The frontal ganglion, therefore, marks the division between the pre-oral cibarium and the post-oral pharynx. It was used by Snodgrass to distinguish between the dilator muscles of the two regions (fig. 1). Snodgrass (1935) also stated that the dorsal series of these muscles is consistently divided by the frontal ganglion connectives into an anterior set of muscles arising on the clypeus and labrum, and a posterior set arising on the frontal and parietal areas of the cranium ; *i.e.* the frontal ganglion connectives pass anteriorly to the retractors of the mouth angles and the first pharyngeal dilators.

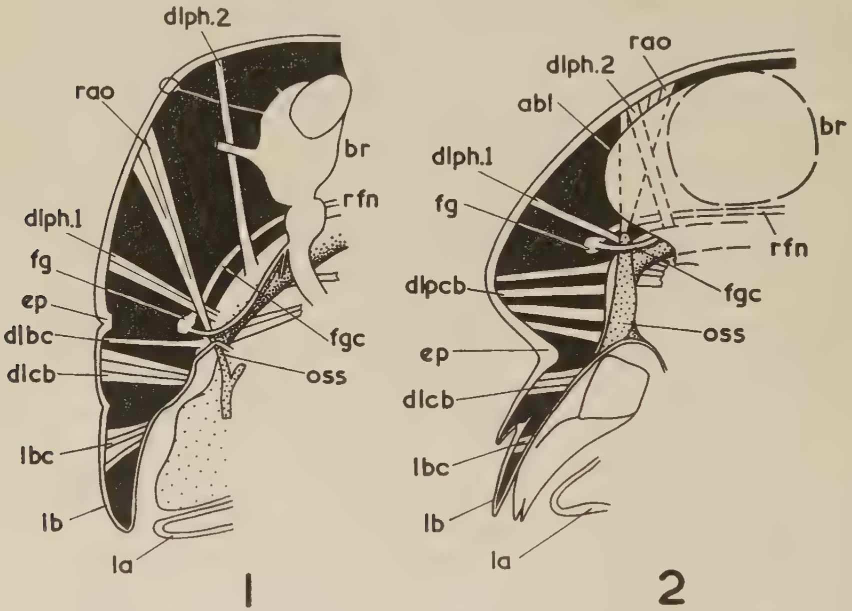
In the beetle *Atomaria ruficornis* (Marsh.) (Evans, 1961), a pair of dilators originates just in front of the epistomal ridge, and a second group of dilators arises posterior to the ridge (fig. 2). Both groups of muscles are inserted anterior to the frontal ganglion connectives and are therefore cibarial dilators. Snodgrass (*loc. cit.*) considered that the epistomal ridge separated the frons and clypeus. Thus in *Atomaria*, the posterior cibarial dilator arises on the frons, a condition which contravenes Snodgrass' criterion regarding the origin of the cibarial dilators.

Snodgrass' definitions were repeated by Dorsey (1943) in a detailed description of the labral, labial and stomodeal musculature of a large number of beetles. However, as pointed out by Ferris (1944), a " recurring discrepancy " is evident when Dorsey's illustrations are considered. In more than half the beetles figured, the posterior cibarial dilators (*m.7* and often *m.6*) originate behind the epistomal ridge upon that part of the head capsule already labelled by Dorsey as the frons. Ferris (*loc. cit.*), and similarly Cook (1944), explained this by postulating a back growth of the clypeal segment and a corresponding reduction of the frons. Thus they described the area termed by Dorsey (and Snodgrass) the clypeus as the anteclypeus (a region which Cook maintained lacked muscle origins), and interpreted the frons of Dorsey as the clypeus.

However, the " anteclypeus " of Ferris and Cook does bear cibarial muscles in some beetles, as in *Atomaria* and several of the beetles described by Dorsey (e.g. *Popillia, Macrobasis*). Ferris' interpretation is difficult to accept unless his theory of head segmentation (criticised by Manton, 1949) is accepted.

Snodgrass (1935) defined the frons as lying between the epistomal ridge and the frontal sutures and bearing the origins of the labral muscles. The cleavage lines (frontal sutures) are probably not retained in any adult beetles, however (Snodgrass, 1947). The muscle origins must be used to define the frons, therefore, and, in addition to the labral muscles, Snodgrass described the anterior pharyngeal muscles and the retractors of the mouth angles as having frontal origins. These usually defined the more posterior part of the frons. The position of the posterior cibarial muscle's origin varies considerably in the Coleoptera described by Dorsey. It could be used to delimit the posterior part of the clypeus if Snodgrass' criterion regarding cibarial muscle origins is rigidly adhered to. On this basis, the epistome would be a transclypeal ridge in some cases. However, in the larva of *Apatides fortis* (Lec.) (Dorsey, 1943 : fig. 109), the posterior cibarial muscle origin lies immediately between that of the ventral labral muscle and the anterior branch of the retractor of the mouth angles. In this case, therefore, the origin of the posterior cibarial muscle is undoubtedly frontal, and Snodgrass' rule that the cibarial dilators can be defined by their origins on the clypeus does not hold invariably.

In the Lepidoptera, DuPorte (1956) described how in *Protoparce quinquemaculata* Haworth the origin of the posterior cibarial dilator is posterior to the transfrontal inflection, *i.e.* in the same region as the anterior pharyngeal dilators. He emphasised that muscles are functional units dependent for their mechanical efficiency on their point of origin upon the skeleton ; with changes in the form of the organs moved by them they must often shift their origins even if this involves crossing a secondary inflection. This has been illustrated by the work of Medvedev (1960) on certain Tenebrionidae, in which some of the anterior dilators (termed pre- and post-oral pharyngeal muscle bundles) were shown to intersect.



Figs. 1–2.—Diagrammatic longitudinal sections to show the fronto-clypeal region and anterior stomodeum, *etc.*, in :

(1) Generalised orthopteroid head (redrawn by permission from Snodgrass : *Principles of insect morphology* (copyright 1935, McGraw-Hill Book Co. Inc.))

(2) *Atomaria ruficornis* (Marsh.) (Col., Cryptophagidae).

It appears that the fronto-clypeal region in Coleoptera must be interpreted with regard to the functioning of the mouthparts and anterior fore-gut. The size and functional requirements of the cibarium will determine the direction of pull, and therefore the point of origin, of the cibarial muscles on the head capsule. The other factor is the structure of the anterior head capsule itself. It seems reasonable to regard the anterior dorsal part of the head capsule as a single fronto-clypeal area which is traversed by the epistomal ridge. This ridge is important mechanically as a brace between the anterior mandibular articulations. Thus its position and shape with regard to the head capsule must depend largely on the mechanical requirements of the mandibles and head capsule, *i.e.* it is not a constant feature, and as demonstrated above it cannot be used to separate the pharyngeal and cibarial dilators.

Although Snodgrass (1947) maintained that the epistomal sulcus was always fronto-clypeal, he did note that " it is clearly a secondary device for strengthening the head wall between the bases of the jaws, and, considering the irregularity of its occurrence, it may be suspected of having been independently developed in some cases." However, although the epistomal ridge is considered to be inconstant in position, it is convenient to refer to the parts of the anterior head capsule anterior and posterior to the ridge as clypeus and frons ; it seems useful to retain these terms, provided it is realised that they have only topographical significance in the epistomal region (as, in fact, Snodgrass (*loc. cit.*) stated with regard to the frons as a whole). This may be illustrated by considering two stages in the life-history of the beetle, *Leptinotarsa decemlineata* (Say). In the adult (Dorsey, 1943 : fig. 111), the epistomal ridge is arched posteriorly, and the fairly large clypeus bears the origins of all the cibarial muscles in accordance with Snodgrass' criterion. In the larva (Dorsey, 1943 : fig. 115), however, the epistomal ridge is straight, giving a short clypeus, and all the cibarial muscles originate upon the frons.

A related point can be considered here. Snodgrass (1935, 1947) defined the frons by the origin of the facial muscles, and held that these muscles in larvae arise between the dorsal cleavage lines. He also maintained that the mandibular and maxillary muscle origins lie outside the cleavage lines. Hinton (1948) showed that this rule did not always hold in the Trichoptera and Lepidoptera, and Chiswell (1955) demonstrated this in certain Diptera. In the larval Coleoptera figured by Dorsey (*loc. cit.*), the cleavage lines usually divide the muscle origins as maintained by Snodgrass. However, in some cases (*e.g.* the larvae of *Dermestes caninus* Germ., fig. 85, and *L. decemlineata* (Say), fig. 115) part of the retractor of the mouth angles arises behind the cleavage line. In the larva of *Oryctes nasicornis* L. (Dahl, 1952), the pair of labral muscles arises partly from the frons and partly from the coronal apodeme, more posteriorly. Conversely, part of the mandibular adductor arises anterior to the cleavage line. From this evidence, it appears that the dorsal cleavage lines in larval Coleoptera do not always determine the postero-lateral limits of the frons (defining this by Snodgrass' criterion of facial muscle origins). This is the view put forward by Hinton (1948) and Chiswell (1955) in other larval endopterygota.

In a recent paper in which he has discussed the head capsule in Coleoptera, DuPorte (1960) has a rather different conception of the frontal region. He notes a progressive reduction in the distance between the antennae and the clypeus, until the antennal sockets in most species come to lie close to, or actually against, the fronto-clypeal sulcus. He interprets this as either a migration of the antennae, or, more likely, the expansion anteriorly of the epifrons (parietals) at the expense of the frons, until the latter is almost or completely suppressed. On this interpretation, the pharyngeal dilators, mouth angle retractors and labral muscles of many species would apparently arise upon the parietals and not the frons. This would also apply to the posterior cibarial dilator in some species. DuPorte's interpretation of the beetle head appears to regard the frons as a well-defined sclerite which is gradually lost, while Snodgrass (1947) regards the frons as the general facial area above the clypeus which carries the facial muscles. Snodgrass has demonstrated that his criteria with regard to muscle origins apply to many orthopteroid and other insects. The purpose of the present paper is merely to emphasise that such criteria, while often applicable, cannot apply invariably to all insects.

SUMMARY AND CONCLUSIONS

It is suggested that, in the absence of other criteria, the frons must be defined by the origins of the facial muscles (following Snodgrass, 1947), but it must be realised that this region is not necessarily homologous in all beetles. Although its postero-lateral borders are usually delimited in larvae by the dorsal cleavage lines (frontal sutures), this is not necessarily so. Again, because the origins of the cibarial dilators are only governed by functional requirements, they may arise upon either clypeus or frons, and they cannot by themselves be used to define either the posterior limits of the clypeus or the anterior limits of the frons. Therefore, in Coleoptera, the fronto-clypeus forms a single functional area usually divided by the epistomal ridge, the actual position of which is determined by functional needs. Since the fronto-clypeal junction cannot readily be defined it is convenient to regard it as represented by the epistomal sulcus, although it must be recognised that this does not divide homologous areas in all beetles.

ACKNOWLEDGMENTS

This paper is adapted from a Ph.D. Thesis started at King's College, London, and completed at Manchester University; I am grateful to Professor J. F. Danielli, F.R.S. and to Professor H. Graham Cannon, F.R.S. for facilities made available. Dr. D. R. Arthur and Mr. J. G. Blower are thanked for their helpful advice and criticism. I am grateful to the Department of Scientific and Industrial Research for a maintenance grant while at King's College, London.

REFERENCES

CHISWELL, J. R., 1955, On the last instar larva of *Tipula livida* van der Wulp (Diptera, Tipulidae) with notes on the fronto-clypeal region of larval Tipulinae and caterpillars. *Proc. R. ent. Soc. Lond.* (A) **30** : 127–36.

COOK, E. F., 1944, The morphology and musculature of the labrum and clypeus of insects. *Microentomology* **9** : 1–35, 18 figs.

DAHL, J., 1952, The musculature of the head and mouth parts of the larva of *Oryctes nasicornis*. *Ent. Medd.* **26** : 196–221, 13 figs.

DORSEY, C. K., 1943, The musculature of the labrum, labium and pharyngeal region of adult and immature Coleoptera. *Smithson. misc. Coll.* **103** (7) : 42 pp., 24 pls.

DUPORTE, E. M., 1956, The median facial sclerite in larval and adult Lepidoptera. *Proc. R. ent. Soc. Lond.* (A) **31** : 109–16, 5 figs.

—— 1960, Evolution of cranial structure in adult Coleoptera. *Can. J. Zool.* **38** : 655–75, 55 figs.

EVANS, M. E. G., 1961, The muscular and reproductive systems of *Atomaria ruficornis* (Marsham) (Coleoptera, Cryptophagidae). *Trans. roy. Soc. Edinb.* **64** : 297–400, 64 figs.

FERRIS, G. F., 1944, On certain evolutionary tendencies in the heads of insects. *Microentomology* **9** : 78–84, 1 fig.

HINTON, H. E., 1948, The dorsal cranial areas of caterpillars. *Ann. Mag. nat. Hist.* (11) **14** : 843–52, 6 figs.

MANTON, S. M., 1949, Studies on the Onychophora. VII. The early embryonic stages of *Peripatopsis*, and some general considerations concerning the morphology and phylogeny of the arthropoda. *Philos. Trans.* (B) **233** : 483–580.

MEDVEDEV, G. S. 1960, The muscles of the mouth-parts and pharyngeal region in Tenebrionidae (Coleoptera) of Turkmenia. *Rev. Ent. URSS* **39** : 69–79

SNODGRASS, R. E., 1935, *Principles of Insect Morphology.* London.

—— 1947, The insect cranium and the "epicranial suture". *Smithson. misc. Coll.* **107** (7) : 52 pp., 15 figs.

LIST OF ABBREVIATIONS

abl, anterior lobe of brain.
br, brain.
dlbc, dilator muscle of buccal cavity.
dlcb, dilator muscle of cibarium.
dlpcb, dilator muscle of posterior cibarium.
dlph.1, first dilator muscle of the pharynx.
dlph.2, second dilator muscle of the pharynx.
ep, epistomal ridge.
fg, frontal ganglion.
fgc, frontal ganglion connectives (frontal nerves).
la, labium.
lb, labrum.
lbc, labral compressor muscle.
oss, oral angle of hypopharyngeal suspensorial sclerite.
rao, retractor muscle of the mouth angles.
rfn, recurrent frontal nerve.

NOTES ON THE LIFE-HISTORY AND HABITS OF *CHONOCEPHALUS DEPRESSUS* DE MEIJERE (DIPTERA : PHORIDAE) IN SOUTH INDIA

By Y. Ramchandra Rao

(29/1, *Nagasandra Road, Bangalore, India*)

During the period 1913 to 1916, when the writer was in charge of the Insectary attached to the Agricultural College and Research Institute, Coimbatore (South India), he first encountered specimens of this wingless Phorid in some of the rearing cages, but little notice was taken of them. In March, 1914, a male found in flight carrying the female *in copula* was collected and several such pairs were later noted in cages containing slices of decaying watermelon.

It was first believed that this fly might prove to be identical with *Chonocephalus fletcheri*, which had been described by Schmitz (1912) from female forms collected by Fletcher from decaying rice stems in December, 1911, in East Bengal. A close examination, however, showed that the Coimbatore forms differed from the description of *fletcheri* in many respects. Nor did the male forms of the phorid quite appear to agree with the description of *Chonocephalus similis* Brues (1905), based on a single male collected from Matheran, Bombay. In June, 1915, specimens of both sexes were sent to Professor J. C. M. de Meijere, at Amsterdam, for determination. In a letter dated 14th September, 1915, Professor de Meijere stated : " Having examined the specimens of *Chonocephalus* of which Mr. Ramchandra has worked out the life-history, I inform you that the female is identical to my *Ch. depressus*, which I described from Medan (Sumatra), but which we also possess from Java. When in my figure the apex of the abdomen is more pointed than usual with your species, the reason is that in my specimen the margin of the tergites was somewhat curved up to the ventral surface. As to the male, I agree with Mr. Ramchandra that it can scarcely be identical with *Ch. similis* Brues, the bristles of the head and the length of the first vein differing from his description ; also Brues' (single!) specimen seems to be somewhat larger and darker. As I did not know the male of my *depressus*, a description of it can be added to the biological notes. Certainly a figure of the wing will be useful ".

The writer regrets very much that, owing to a combination of circumstances, he has been unable till now to publish the life-history notes and to give a description of the male of *Ch. depressus.*

Life-history and Habits

Life-history.—The species was found to breed in the neighbourhood of Coimbatore in various types of rotting vegetable matter, but its favourite medium appeared to be the pulp of rotting fruits. The wingless female has the habit of moving about in characteristically jerky fashion, pecking at fruit pulp here and there like a hen. While feeding on the fruit, the female may be found extruding its short ovipositor and depositing its eggs just under the surface film of the pulp (fig. 2). Eggs are usually laid singly, but sometimes in groups.

Egg.—A tiny object, elongate oval in shape, about 0·3 mm. in length, and creamy white in colour. Under the high power of the microscope, the chorion, which is transparent, is seen to be made up of a layer of hexagonal cells (fig. 1). Translucent in the beginning, the eggs turn opaque as the developing embryo assumes shape.

The temperatures are very mild at Coimbatore during the cold weather (December and January), when the daily means range from 23° to 26° C. (73–79° F.), and the eggs generally took two days to hatch out at this time.

Larva (fig. 3).—The newly-hatched larva is about 0·5 mm. long, slender and elongate, and of glassy transparency. In general build, it more or less resembles the full-grown larva, except in the absence of the anterior spiracles. Soon after hatching, the larva begins to wriggle about in the rotting pulp and as it feeds, it begins to grow in size. It is presumed that there are in this species, as in the case of many flies, three larval instars, but the moults have not been followed through.

The larva of the last instar, when full-grown, measures about 3 mm. inclusive of the extended tail. The coloured contents of the internal organs clearly show out through the transparent skin. The body is cylindrical, but tapers to a point both anteriorly and posteriorly. The hind end of the body terminates in the highly retractile, telescopic tail, resembling the rat-tail of the *Eristalis* larva, which when fully extended is nearly as long as the body. Dorsally and laterally, the segments of the larva (except the anterior ones) bear each a transverse band of close-set cilia-like processes. The mouth is armed with a pair of dentate hooks. The anterior spiracles appear as single finger-like processes on either side. The longitudinal tracheal trunks are continued into the tail and end in a common spiracle, protected at the tip by a circlet of hairs which serve to keep the water out. While feeding the larvae dive deep into the rotting fruit and swing their bodies about, but always keep the tip of the tail projecting beyond the surface film so as to obtain air.

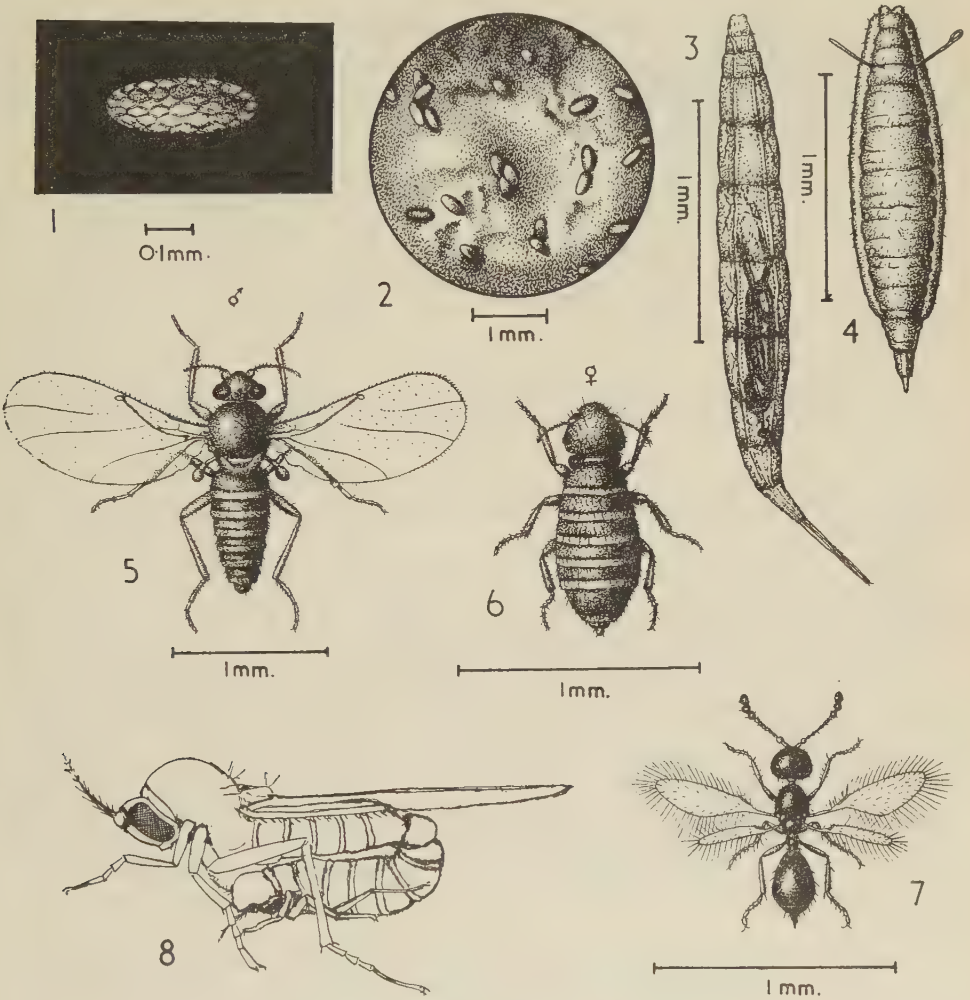
When fully fed, the larva leaves the liquid filth and wanders about seeking a comparatively dry place for pupation. It is now pale yellow in colour and exhibits the habit of doubling itself up and, with a sudden jerk, flicking itself off to some distance on the ground. The larval period would appear to vary from 8 to 14 days, with an average of 10 days.

Puparium (fig. 4).—The puparium is somewhat spindle-shaped, ending rather bluntly at the anterior end, but posteriorly terminating in a pointed tail, at the tip of which spiracles are borne. It is about 1·5 mm. long. The body is rather depressed, but the segments are distinct. The puparium is characterised by the presence of a pair of obliquely directed horn-like rods on its anterior half. The function of these processes is believed to be of a respiratory nature, since wherever the puparia happen to form in a semi-liquid medium, the horn is actually seen to form the stem of a tracheal trunk from which branches are given off at intervals, all these being found floating on the semi-liquid medium. Obviously, these plumose branches represent parts of the larval tracheal system cast off at the time of the final moult. Wherever puparia are formed in dry situations, the tracheal trunk with the branches breaks off, leaving only the horn-like stems behind.

In the case of females, the duration of the pupal stage is 7–8 days, and in the male, 9–10 days.

Adult (figs. 5 and 6).—There is a strongly pronounced sexual dimorphism, the male exhibiting typical phorid wing venation, while the female is wingless and looks like an immature psocid. The male is characterised by large eyes, prominent thorax and well developed legs, whereas the female has only feebly developed eyes, a degenerate thorax and shorter legs. In the female, the abdomen is yellowish- to greyish-brown and each of the visible segments except the sixth carry at the hind border a conspicuous dusky band, bearing at its hind edge a row of fairly large, clear, bright circular spots (visible, however, only in transmitted light), each giving rise to a bristle. The latter are absent in the male, though dusky bands are present. The male is darker than the female. The female is about 1 mm. long, the male about 1·5 mm. in length and 2·5 mm. in wing-expanse; there is much variability in size in both sexes.

The adults were found emerging generally in the forenoon, and began to feed almost immediately ; in the afternoon they became active. The males were found feverishly running from place to place and flying from one side of the cage to the other. If in the course of his activity the male happened to sight a female moving about in her usual jerky manner, he was found to circle round her for a time and then suddenly pounce on her. Pairing took place immediately. The mating pair presented a rather singular spectacle : except for the fact that the abdomen of the male appeared somewhat bulged, the female for all practical purposes vanished from sight. In fact, her legs neatly folded on the sides of her body, she looked as if she had been glued to the abdomen of the male, who bore her whole weight (fig. 8). The male flies actively while *in copula*, and this recalls similar habits among the Mutillidae, where, however, the female is supported by the legs of the male during flight. It is not unlikely that this may serve to widen the range of distribution of the species. After a time, the female drops off and the male flies away.



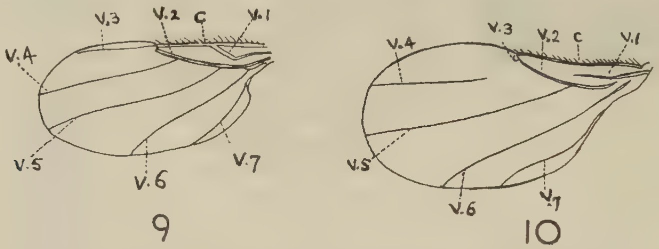
Figs. 1–8.—(1–6) *Chonocephalus depressus* de Meij.: (1) egg, enlarged ; (2) eggs in rotting fruit pulp ; (3) mature larva ; (4) puparium ; (5) male ; (6) female. (7) undetermined proctotrupid parasite attacking puparia of *C. depressus.* (8) *C. depressus :* pair *in copula.*

Distribution.—So far the writer has noted the presence of this species at Coimbatore and at one or two places in Coorg, but it is quite likely that it may be widely distributed in South India. At Coimbatore, it has been collected from rotting fruits of Cucurbitaceae in the field, but it might thrive better in situations sheltered from sun and rain.

Natural enemies.—Some of the puparia found in cages at the Insectary were found attacked by a small black proctotrupid wasp (fig. 7).

DESCRIPTION OF THE MALE

In 1926, figures were prepared illustrating the life-history of the insect and showing the differences between the male and the female. Since then much of the original material has been lost, with the exception of several slides of males and females mounted in balsam, and the following notes are based on the original drawings and on these slides.



FIGS. 9–10.—(9) Wing venation of *Puliciphora pusillima* de Meijere (after de Meijere 1912). (10) Wing venation of *Chonocephalus depressus* de Meijere, male ; Coimbatore.

The figure given by Professor de Meijere in the description of *Puliciphora pusillima* de Meij. (fig. 9) may be taken as typical of phorid venation. Important constituents eight in number, made up of the costa, at anterior rim of wing, and seven longitudinal veins.

Of these, costa and veins I and II, which are all parallel, and strongly developed, extend only up to about middle of anterior edge of wing, but veins III, IV, V, VI, and VII, all branching from vein II, reach posterior border of wing. In certain genera of Phoridae, there are cross-veins at the anterior part of the wing, but in *Chonocephalus* the venation is fairly simple. Vein I (figs. 5 and 10) branches off from basal part of vein II and after a slight bend, passes forward parallel to costa, but fades off slightly beyond middle of costa ; vein II somewhat sinuate, joining distal end of costa about middle of wing ; a small ring-like cell at junction of vein II with costa, surrounded by a faint circular vein emerging from tip of vein II (fig. 10) ; presumably this represents vein III of *Puliciphora ;* vein IV slightly curved, fading out towards its basal fourth ; vein V nearly straight, veins VI and VII somewhat curved. Wings closely covered with numerous microscopic hairs.

Comparison of the description given by Brues (1905) for *Ch. similis* with the male of *Ch. depressus* shows that there is a great deal of similarity in coloration and wing-venation (with the exception of the circular cell, which Brues did not mention), though there are apparently also some differences in respect of the head bristles, and the length of vein I. In view of the above similarities it is doubtful whether these can be considered to be separate species without an examination of the type specimen of Brues and a comparison with other described *Chonocephalus* species.

ACKNOWLEDGMENTS

The writer wishes to acknowledge the kind help received in the past from Mr. E. Ballard, then Government Entomologist at Coimbatore, during the life-history studies and from Professor J. C. M. de Meijere, Amsterdam, in identifying the phorid and sending literature on the subject. Recently he also received much help by way of facilities for the microscopical examination of slide material and a loan of literature from Dr. M. Puttarudraiah, Mysore Government Entomologist and Mr. Syed Usman, Senior Assistant Entomologist, Bangalore and from Dr. V. P. Rao, Commonwealth Institute of Biological Control, Bangalore Laboratory, to all of whom he wishes to express his gratefulness. Last but not least, he wishes to acknowledge with thanks the kind help received from Sir Boris Uvarov, London, by his going through the draft of the paper and suggesting valuable alterations.

REFERENCES

BRUES, C. T., 1905, Phoridae from the Indo-Australian region. *Ann. Mus. Nat. Hungar.* **3** : 554–5.

—— 1906, *Phoridae, in* Wytsman, P., *Genera Insectorum.* Brussels.

DE MEIJERE, J. C. M., 1912, Über die Metamorphose von *Puliciphora* und über neue Arten der Gattungen *Puliciphora* Dahl und *Chonocephalus* Wandolleck. *Zool. Jahrb.*, Suppl. **15** : 141–54.

SCHMITZ, VON H., 1912, *Chonocephalus fletcheri*, n. sp. *Zool. Anz.* **39** : 727–29.

A PEARL-EYED MUTATION IN *GNATHOCERUS CORNUTUS* (FAB.) (COLEOPTERA : TENEBRIONIDAE), WITH NOTES ON SIMILAR VARIANTS IN OTHER BEETLES

By C. E. Dyte and Dorothy G. Blackman
(*A.R.C. Pest Infestation Laboratory, Slough, Bucks.*)

Introduction

Many of the beetles which infest stored food products are easy to culture and are commonly used as experimental subjects. A number of mutations have been reported in these beetles, notably in *Tenebrio molitor* L. and *Tribolium* spp. If viable, such mutants have potential value as marked individuals in short-term ecological experiments.

In the present paper a pearl-eyed mutation in the Broad-horned Flour Beetle, *Gnathocerus cornutus* (Fab.) is described, and the existence of similar phenotypes in other beetles is discussed. No mutations in *G. cornutus* appear to have been described previously, though this species is a well known pest of flour-mills, and has been used in laboratory population studies.

Materials and Methods

Sources of material

Pearl-eyed *G. cornutus* were first noticed in a laboratory culture of insects used for tests with insecticides. This culture came from a stock of unrecorded origin which has been maintained in this laboratory for about ten years. A pure culture of the pearl-eyed form was obtained by isolating pharate adults in which the eyes lacked colour.

Other cultures of this species maintained at the Laboratory were also found to contain some pearl-eyed individuals. For the test crosses, therefore, a culture of normal beetles was established from individuals collected from a flour mill at Belfast, N. Ireland. No pearl-eyed individuals have been found in this normal stock during seven generations of laboratory culture.

Description of the mutation

Pearl-eyed *G. cornutus* are similar to pearl-eyed *Tribolium*. The eyes are pearl-coloured, instead of being black as in the normal phenotype, though a narrow band of peripheral facets (the width of which depends on the angle of vision) appears black. On dissection from the medial side the black appearance of the outer facets can be seen to be due to the dark pigmentation of the underlying ocular diaphragm, as in pearl-eyed *Latheticus* and *Tribolium* (Wolsky and Zamora 1960 ; Graham 1957).

The pigmented ocelli, present in normal *G. cornutus* larvae, cannot be seen in the larvae of the pearl-eyed mutant. We have not made histological preparations to determine whether these larval ocelli are absent, or merely lacking in pigment. This question does not appear to have been resolved in the larvae of any of the pearl-eyed beetle mutants.

Methods

The male pupae of *G. cornutus* can be distinguished by the prominent dorsal tooth on the mandibles. For all the test crosses single pairs were isolated in 3×1 inch glass vials containing about 10 g. of food medium, comprising 70 per cent. whole wheat flour, 28 per cent. rolled oats and 2 per cent. dried yeast. The vials and stock cultures were maintained at 25°C. and 75 per cent. R.H. The vials were left for three weeks, during which adults emerged and laid eggs. These adults were then removed, and thereafter adults of the daughter generation were removed and examined.

RESULTS

The results of most of the test crosses made are shown in Table I. The first two sets of crosses between normal and pearl-eyed beetles yielded 244 beetles, all with normal eye colour. When these F_1 normal beetles were crossed *inter se* (cross 3), 280 normal and 87 pearl-eyed beetles were produced. This does not differ significantly from the 3 : 1 ratio expected with a single recessive gene ($\chi^2=0\cdot328$; $P=0\cdot5$–$0\cdot7$). There is no evidence of sex linkage.

TABLE I.—*Summary of test crosses*

Cross Number	Parents		Pairs set up	Infertile pairs	Offspring			
					Normal		Pearl	
	Male	Female			Male	Female	Male	Female
1 .	normal ×	pearl	10	3	87	78	0	0
2 .	pearl ×	normal	10	4	48	31	0	0
	Total (1 and 2)		20	7	135	109	0	0
3 .	F_1 normal ×	F_1 normal	26	6	145	135	43	44
	Total (3)				280		87	
4 .	F_2 pearl ×	pearl	5	2	0	0	19	20
5 .	pearl ×	F_2 pearl	5	0	0	0	23	34
	Total (4 and 5)		10	2	0		86	

When the F_2 pearl-eyed beetles were back-crossed to pearl-eyed beetles from the stock culture, only pearl-eyed beetles were produced (crosses 4 and 5). In addition, thirty normal phenotypes from the F_2 generation were backcrossed to homozygous pearl-eyed beetles. Thirteen of these pairs proved infertile, and two others produced only single offspring (one pearl-eyed, the other normal). Of the remaining fifteen pairs, two produced only normal progeny, and the other thirteen each yielded both pearl-eyed and normal offspring. These thirteen pairs produced in all 78 normal and 96 pearl-eyed progeny, which is in reasonable agreement with the 1 : 1 ratio expected when heterozygote and homozygote are crossed ($\chi^2=1\cdot86$, $P=0\cdot1$–$0\cdot2$). Thus thirteen of these normal F_2 phenotypes can be classified as heterozygotes and two as homozygotes. This classification does not deviate significantly from the expected ten heterozygotes and five homozygotes ($\chi^2=2\cdot70$, $P=0\cdot10$).

These results indicate that the inheritance of pearl-eye in *Gnathocerus cornutus* is governed by a single, recessive, autosomal gene for which the name " pearl " and symbol **pp** are proposed.

OTHER PEARL-EYED BEETLES

Pearl-eyed mutants have previously been reported in the Tenebrionidae and Dermestidae. Graham (1957) and Wolsky and Zamora (1960) have sectioned pearl-eyed individuals of *Tribolium* spp. and *Latheticus oryzae* Waterh., and they consider that the dark appearance of the outer eye facets in these pearl-eyed beetles is due to the underlying ocular diaphragm, which is deeply pigmented. Sokoloff (1959*a et seq.*) reported that in the pearl mutants of *Tribolium castaneum* (Hbst.) and *Latheticus oryzae* the ocelli of the larvae cannot be seen because they are unpigmented (or absent). The pearl mutation in *Gnathocerus cornutus* thus has similar effects to the pearl mutations in these other Tenebrionids.

The examination of adult beetles from cultures of other species maintained at the Pest Infestation Laboratory has revealed pearl-eyed individuals of *Tenebrio molitor* L. (Tenebrionidae), *Carpophilus dimidiatus* (F.) (Nitidulidae), *Cryptolestes turcicus* (Grouv.) (Cucujidae) and *Dermestes maculatus* Deg. (Dermestidae). The inheritance of these forms has not been studied by us, but pure cultures of the first three have been established, and in these the ocelli of the mutant larvae were found to be unpigmented (or absent) as in the laboratory stock of pearl *Tribolium confusum* Duval. This last stock was isolated from the same cultures as those from which Graham (1957) originally described " pearl " in this species.

Pale eyed mutants of *Tenebrio molitor* and *Dermestes maculatus* have previously been described by Ferwerda (1928) and Philip (1940). Philip states that the mutation " white eye " which she describes in *D. maculatus* is comparable to " pearl " in *Tribolium castaneum*. The same would appear to be true of " fleischfarbenen Augen " in *Tenebrio molitor*. Both of these mutations are autosomal, and their effects on adult eye colour are recessive. In the absence of contrary evidence we have assumed that the pearl-eyed individuals of these two species which we have observed are homozygous for the genes described by these writers, and they are considered as such in Table II.

TABLE II.—*Coleoptera in which pearl-eyed adults have been found*

Species	Mode of inheritance	Gene symbol proposed	Larval ocelli unpigmented	References
TENEBRIONIDAE				
Tribolium castaneum (Hbst.)	Autosomal recessive	*pp*	Yes	Park (1937), Sokoloff (1959*a*).
Tribolium confusum Duv.	Autosomal recessive	*pp*	Yes*	Graham (1957).
Latheticus oryzae Waterh.	Autosomal recessive	*pp*	Yes	Sokoloff (1959*b*, *c*).
Gnathocerus cornutus (F.)	Autosomal recessive*	*pp**	Yes*	*
Tenebrio molitor L.	Autosomal recessive	*gg*	Yes*	Ferwerda (1928).
DERMESTIDAE				
Dermestes maculatus Deg.	Autosomal recessive	*ww*	?	Philip (1940).
Trogoderma granarium Everts	Autosomal recessive	*pp*	Yes†	Reynolds and Sylvester (1961).
NITIDULIDAE				
Carpophilus dimidiatus (F.)	?	.	Yes*	*
CUCUJIDAE				
Cryptolestes turcicus (Grouv.)	?	.	Yes*	*

* Observations reported in the present paper.

† The frontal ocellus in the adult of this species is also unpigmented.

DISCUSSION

The existence of the mutation pearl (**pp**) in *Gnathocerus cornutus* brings the number of Tenebrionidae in which this type of gene has been recorded to five species in four genera. In each case the pearl gene affects the appearance of both the compound eye of the adult, and the ocelli of the larva, and is inherited as an autosomal recessive.

Marshall (1927), working with *Tribolium confusum*, rejects the view that the pigment from the ocelli of the larva migrates to the compound eyes during development. He found that the larval ocelli move to near the apex of the optic lobe of the brain during pupation. They can be found there in the adult together with their pigment granules. The pigment of the compound eyes of *Tribolium* is thus formed *de novo* in the pupal stage. It appears therefore that the larval and adult expressions of the pearl gene are distinct, though it is possible that a single biochemical mechanism is involved.

According to Bishop (1960), the pigment from the larval ocelli in *Cryptolestes* spp. moves posteriorly, shortly before pupation, to near the base of the fleshy portion of the prothoracic silk gland. We have been able to confirm this observation in *Cryptolestes turcicus* (Grouv.). In the pearl-eyed form of this species no pigment is visible near the base of the silk gland of late fourth instar larvae. The silk glands, however, appear to function normally and a cocoon is formed.

Existing information on pearl-eyed Coleoptera is summarised in Table II. The existence of similar inherited variations in representatives of four families of beetles is of interest in relation to comparative genetics. Haldane (1927) has suggested, on the basis of similarities in the inheritance of some coat-colours, that certain genes in carnivores and rodents might be homologous. Such suspected homologies can only be proved in genera where interspecific crosses are possible (e.g. *Drosophila*), and Haldane's view has been criticised by Huxley (1942 : 511) on the grounds that parallel variation may be due to non-homologous mutations producing parallel character change. However, the information on coat-colour inheritance in mammals which has accumulated in the last thirty years has demonstrated further apparent homologies (Little, 1958) and these are not limited to genes concerned with coat-colour characters. For instance, Searle (1953) suggests that the normal allelomorph of the " split-hand " mutant existed in cretaceous mammals, since this defect occurs in both modern carnivores and modern primates.

The " pearl " beetle mutants may present a parallel case. If these mutations are in fact homologous, and the phylogenetic studies of Crowson (1960) are accepted, then the normal allelomorph of " pearl " would appear to have been part of the heritable make up of certain polyphagan beetles in the early Jurassic period. On the other hand, the apparent similarities in the different pearl-eyed beetles may have arisen as a result of non-homologous mutations producing parallel phenotypic effects.

ACKNOWLEDGMENT

We are indebted to Mr. J. Thompson for sending us living *Gnathocerus cornutus* from a Belfast flour-mill.

SUMMARY

The mutation " pearl " in *Gnathocerus cornutus* (Fab.) is described. It is inherited as a single autosomal recessive gene. The compound eyes of " pearl " homozygotes are pearl-coloured, and in the larvae of these homozygotes the ocelli are not discernible.

Similar mutants occur in four other tenebrionids and two dermestids, though the larvae of one of the latter have not been studied. Similar phenotypes are reported in the Nitidulidae and Cucujidae and are inherited, though the mode of inheritance has not been investigated. All these mutations may be homologous.

REFERENCES

BISHOP, G. W., 1960, Taxonomic observations on the larvae of the three American *Cryptolestes* (Coleoptera : Cucujidae) that infest stored grain. *Ann. ent. Soc. Amer.* **53** : 8–11.

CROWSON, R. A., 1960, The Phylogeny of Coleoptera. *Ann. Rev. Ent.* **5** : 111–34.

FERWERDA, F. B., 1928, Genetische Studien am Mehlkäfer *Tenebrio molitor* L. *Genetica* **11** : 1–110.

GRAHAM, W. M., 1957, Pearl eye in the Confused Flour Beetle, *Tribolium confusum* Duval (Tenebrionidae). *Ent. mon. Mag.* **93** : 73–5.

HALDANE, J. B. S., 1927, The comparative genetics of colour in Rodents and Carnivora. *Biol. Rev.* **2** : 199–212.

HUXLEY, J., 1942, *Evolution : the modern synthesis.* London.

Little, C. C., 1958, Coat colour genes in rodents and carnivores. *Q. Rev. Biol.* **33** : 103–37.

Marshall, W. S., 1927, The development of the compound eye of the Confused Flour Beetle, *Tribolium confusum* Jacq. *Trans. Wisc. Acad. Sci. Arts Lett.* **23** : 611–630.

Park, T., 1937, The inheritance of the mutation " pearl " in the flour beetle, *Tribolium castaneum* Herbst. *Amer. Nat.* **71** : 143–57.

Philip, V., 1940, A genetical analysis of three small populations of *Dermestes vulpinus* F. (Coleoptera). *Proc. Indian Acad. Sci.* **12** : 133–71.

Reynolds, E. M. and Sylvester, N. K., 1961, Pearl mutant in *Trogoderma granarium* Everts. (Dermestidae). *Tribolium Inform. Bull.* **4** : 25

Searle, A. G., 1953, Hereditary " split-hand " in the domestic cat. *Ann. Eugen., Lond.* **17** : 279–82.

Sokoloff, A., 1959*a*, The nature of the " pearl " mutation in *Tribolium castaneum* Herbst. *Amer. Nat.* **93** : 329–31.

—— 1959*b*, The " pearl " gene in *Latheticus oryzae* Waterh. *Ibid.* **93** : 394–6.

—— 1959*c*, The genetics of " pearl " in *Latheticus orzyae* Waterh. *Canad. J. Genet. Cyt.* **1** : 183–8.

Wolsky, A. and Zamora, R., 1960, The structure of the " pearl " eye of *Latheticus oryzae*. *Amer. Nat.* **94** : 309–12.

Book Notices.

Termites. Their recognition and control. By W. V. Harris. 8vo. London (Longmans), 1961. Pp. xii, 187 ; text-illust. £2.

The purpose of this work is to assist the diagnosis of termite damage and to suggest measures for its prevention and control. It is an account of termite damage as a world problem.

The early chapters deal with the natural history of termites and the means of their identification, and are intended to serve as an introduction to the chapters which follow, in which descriptions of the various groups, the genera most commonly causing damage and their geographical distribution are given ; the final chapter deals with damage to materials other than timber, such as paper, fabrics and plastics.

The book contains lists of the species of termites attacking crops, forest trees and constructional timber in buildings. Methods for the prevention of termite attack are discussed and an appendix gives details of various chemicals used in termite control. There are also a number of text-figures, half-tone photographs, coloured plates, a bibliography and a general index.

Insect Sounds. By P. T. Haskell. 8vo. London (H. F. & G. Witherby Ltd.), 1961. Pp. viii, 189 ; text illust. 30s.

The aims of this work are to provide teachers and students with a short outline of the present day knowledge of insect sounds, to illustrate the most important general principles and integrate the subject into the wider fields of ethology and entomology, and to arouse interest in the problems that await investigation.

The various chapters deal with the recording and analysis of insect sounds, sound-producing mechanisms, insect hearing, their song patterns, behaviour associated with sound, physiological aspects of acoustic behaviour, and a brief general assessment of the part played by sound in the insect world.

The work contains an index, a brief list of references and a number of plates and text figures.

INDEX

acanthopygia, Chelidurella, 23
Acanthoscelides obtectus, 150
acasta, Melittobia, 103
advena, Ahasverus, 148
Aeolothrips albicinctus, 89
— fasciatus, 89
— gloriosus, 89
— melaleucus, 90
— tenuicornis, 89
affine, Mezium, 152
africana, Mansonia, 113
Agapetus fuscipes, 43, 44, 45
agarithe, Phoebis, 49–56
Agrypnia pagetana, 39, 43, 44
Ahasverus advena, 148
albicintus, Aelothrips, 89
albicorne, Odontocerum, 43, 45
albicornis, Aphycus, 111
Allomachilis, 84
Alphitobius diaperinus, 148
— laevigatus, 148
Alphitophagus bifasciatus, 144, 148
americanus, Dinocampus, 101
Anabolia nervosa, 43
Anagyrus schonherri, 111
analis, Callosobruchus, 150
anaphe, Tribolium, 147
angustata, Molanna, 37, 43, 44, 45, 46
Anisolabis littorea, 22, 23, 25
annulatus, Drusus, 43, 45, 58, 61
annulipes, Euborellia, 22
— Hoplandrothrips, 92
anthrenoides, Trogoderma, 151
Apatania muliebris, 43, 45
Apatides fortis, 159–60.
Aphelocheirus, 63
aphidivora, Phaenobremia, 126, 129
Aphycus albicornis, 111
Apis mellifera, 5
Aptinothrips obscurus, 90–91
— rufus, 90
— stylifer, 90
arachidis, Marava, 22, 23
Araecerus fasciculatus, 144, 150
Arixenia esau, 21–25
— jacobsoni, 21–25
arsames, Olynx, 103, 107–110
aterrima, Athripsodes, 43
Athripsodes aterrima, 43
— cinerea, 42, 45, 57–58, 59, 61
— senilis, 57–58, 61
Atomaria ruficornis, 159
atratus, Taeniothrips, 91, 93
auratus, Torymus, 111

barnesi Tricholaba, 126, 129
Beraea maurus, 42, 45
Beraeodes minuta, 43, 45
bicolor, Triaenodes, 43, 61
bidens, Hoplandrothrips, 92
bifasciatus, Alphitophagus, 144, 148
binodosa, Blaesoxipha, 67–68
bipunctatus, Limnephilus, 37
Blaesoxipha binodosa, 67–68
boltoni, Glossosoma, 43, 45
Brachycentrus subnubilis, 43, 45, 58, 59, 61
brevistylis, Petrobius, 81, 84, 86
Bryocoris pteridis, 64

cacoeciae, Trichogramma, 111
Caddis flies, 37–46
Callosobruchus analis, 150
— chinensis, 150
— maculatus, 150
— rhodesianus, 150
capensis, Cryptolestes, 149
Carpophilus dimidiatus, 150, 170
— hemipterus, 150
Caryedon gonagra, 150
castaneum, Tribolium, 147, 148, 169, 170
Cataloipus oberthuri, 67–68
Cathartus quadricollis, 148
centralis, Limnephilus, 43, 45
cerealium, Limothrips, 90, 93
Chaetopteryx villosa, 42, 43, 45
Chelidurella acanthopygia, 23
Chelisoches morio, 23
chinensis, Callosobruchus, 150
Chirothrips hamatus, 90
— manicatus, 90
Chonocephalus depressus, 163–6
Chrotogonus trachypterus, 1–4
ciliaris, Notidobia, 42, 43, 45, 57, 58–59
cinerea, Athripsodes, 42, 45, 57–58, 59, 61
—Phryganea, 45
cingulatus, Torymus, 111
coccinellae, Dinocampus, 96, 97, 98, 99
Comedo larvarum, 110
— larvarum *f.* nigribasis, 110
confusum, Tribolium, 147, 170
consociatus, Taeniothrips (Rhopalandrothrips), 91
conspersa, Triaenodes, 37
coriaceus, Euphlaeothrips, 92
Corixa punctata, 119–25
cornutus, Gnathocerus, 148, 168–71
Crunoecia irrorata, 43, 45
Cryptolestes *spp.*, 171
— capensis, 149
— ferrugineus, 148–9
— pusilloides, 148–9
— pusillus, 148–9

Cryptolestes turcicus, 148–9, 170, 171
— ugandae, 148–9
Ctenolepisma, 83
CULICIDAE, 113–7
cytisi, Odontothrips, 91

Dasyneura *sp.*, 133
— gentneri, 126–9
— leguminicola, 126–9
decemlineata, Leptinotarsa, 161
decipiens, Limnephilus, 58
delanyi, Machiloides, 81–87
Dendrothrips ornatus, 90
denticornis, Limnothrips, 90
depressus, Chonocephalus, 163–6
Dermestes frischii, 144, 151
— haemorrhoidalis, 144, 151
— lardarius, 144, 151
— maculatus, 144, 151, 170
destructor, Tribolium, 147
diaperinus, Alphitobius, 148
dimidiatus, Carpophilus, 150, 170
Dinocampus americanus, 101
— coccinellae, 96, 97, 98, 99
— rutilus, 96, 97, 98
distinguendus, Haplothrips, 92
Dixippus, 64
Dolichonabis limbatus, 65
dominica, Rhizopertha, 150
Drusus annulatus, 43, 45, 58, 61
dubius, Perilitus, 96–101

esau, Arixenia, 21–25
eubele, Phoebis, 49, 50
Euborellia annulipes, 22
— stali, 23, 25
euedoreschus, Olynx, 103, 104–6
Euphlaeothrips coriaceus, 92
Eurytoma robusta, 155–6, 157
— serratulae, 153–4, 155, 156
— strigifrons, 156, 157
— tibialis, 154–5, 156

fasciatus, Aeolothrips, 89
fasciculatus, Araecerus, 144, 150
ferrugineus, Cryptolestes, 148–9
ferus, Nabis, 64
flavicornis, Limnephilus, 43, 45, 58, 60
— Molanna, 45
Forficula auricularia, 22, 23
fortis, Apatides, 159–60
Frankliniella intonsa, 92, 93
— tenuicornis, 92
fraseri, Mansonia, 113
frischii, Dermestes, 144, 151
fungi, Phlaeothrips, 92
furcata, Mesovelia, 64
fuscicornis, Limnephilus, 42, 43, 45
fuscipennis, Thrips, 91
fuscipes, Agapetus, 43, 44, 45,
fuscopennata, Mansonia, 113, 114, 115–7
fuscus, Melanthrips, 89, 93

Gall midges, 126–30
gallarum, Olynx, 103, 107, 111
gallarum *f.* pulchra, Olynx, 107, 111
gentneri, Dasyneura, 126–9
Gerris odontogaster, 64
Gibbium psylloides, 152
glabrum, Trogoderma, 151
globulus, Trigonogenius, 152
gloriosus, Aeolothrips, 89
Glossina swynnertoni, 9–20, 69–74
Glossosoma boltoni, 43, 45
Glyphotaelius pellucidus, 43, 44, 45, 58
Gnathocerus cornutus, 148, 168–71
— maxillosus, 148
Goëra pilosa, 43, 44, 45
gonagra, Caryedon, 150
graminum, Stenothrips, 91–92, 93
granarium, Trogoderma, 151
granarius, Sitophilus, 148
grandis, Phryganea, 37, 39, 43, 44, 58, 60
gregaria, Schistocerca, 79
Gryllus, 64

haemorrhoidalis, Dermestes, 144, 151
Halesus radiatus, 43
hamatus, Chirothrips, 90
Haplothrips distinguendus, 92
— setiger, 92
— subtilissimus, 92
Hemimerus talpoides, 25
hemipterus, Carpophilus, 150
Henria psalliotae, 133–42
Heteropeza pygmaea, 141
HETEROPTERA, 63–65
hilleri, Pseudeurostus, 152
hirtum, Lepidostoma, 43, 45
Honey-bees, 5–8
Hoplandrothrips annulipes, 92
— bidens, 92
hukkineni, Thrips, 91
Humbe tenuicornis, 75–80

Ilyocoris, 63, 124
imaginis, Thrips, 94
inclusum, Trogoderma, 151
intonsa, Frankliniella, 92, 93
irrorata, Crunoecia, 43, 45
Ischnodemus sabuleti, 64

jacobsoni, Arixenia, 21–25

Kakothrips robustus, 92

Labidura riparia truncata, 23
lacustris, Oecetis, 43, 45, 57–58, 59, 61
laevigatus, Alphitobius, 148
lardarius, Dermestes, 144, 151
larvarum, Comedo, 110
larvarum *f.* nigribasis, Comedo, 110
Lasioderma serricorne, 144, 150
Latheticus, 168
— oryzae, 147, 148, 169
latipennis, Potamophylax, 43, 45
lativentris, Megathrips, 92
leguminicola, Dasyneura, 126–9
Lepidostoma hirtum, 43, 45
Leptinotarsa decemlineata, 161
Leptosyna, 141
Lestodiplosis trifolii, 129
limbatus, Dolichonabis, 65

Limnephilus bipunctatus, 37
— centralis, 43, 45
— decipiens, 58
— flavicornis, 37, 43, 45, 58, 60
— fuscicornis, 42, 43, 45
— lunatus, 44, 58, 60
— marmoratus, 37
— vittatus, 43, 45
Limothrips cerealium, 90, 93
— denticornis, 90
littorea, Anisolabis, 22, 23, 25
Locusta migratoria migratorioides, 79
Locustana pardalina, 79
longicornis, Mystacides, 45, 57–58, 59, 61
lunatus, Limnephilus, 44, 58, 60

Machiloides delanyi, 81–87
Macrobasis, 159
maculatus, Callosobruchus, 150
— Dermestes, 144, 151, 170
madens, Tribolium, 147, 148
major, Thrips, 91
manicatus, Chirothrips, 90
Mansonia africana, 113
— fraseri, 113
— fuscopennata, 113, 114, 115–7
— metallica, 113, 114–5
— uniformis, 113
Marava arachidis, 22, 23
marmoratus, Limnephilus, 37
mauritanicus, Tenebroides, 151
maurus, Beraea, 42, 45
maxillosus, Gnathocerus, 148
Megathrips lativentris, 92
melaleucus, Aeolothrips, 90
Melanoplus, 79
Melanthrips fuscus, 89, 93
Melittobia acasta, 103
mellifera, Apis, 5
mercator, Oryzaephilus, 148
meridionalis, Odontothrips, 91
Mesovelia furcata, 64
metallica, Mansonia, 113, 114–5
Mezium affine, 152
Miastor, 129
Microvelia *spp.*, 65
migratoria migratorioides, Locusta, 79
migratorioides, Locusta migratoria, 79
minor, Trichostegia, 39, 43
minuta, Beraeodes, 43, 45
minutum, Trichogramma, 111
Molanna angustata, 37, 43, 44, 45, 46
— flavicornis, 45
molitor, Tenebrio, 147, 168, 170
Mosquitoes, 27–35 ; *list of spp. considered*, 30–31
muliebris, Apatania, 43, 45
Mycophila, 141
— speyeri, 141
Mystacides longicornis, 45, 57–58, 59, 61
— nigra, 43, 45

Nabis ferus, 64
nasicornis, Oryctes, 161
Necrobia rufipes, 150
Neides tipularius, 64
nervosa, Anabolia, 43
Neuronia postica, 37
nigra, Mystacides, 43, 45
f. nigribasis, Comedo larvarum, 110
nigricornis, Silo, 42, 43, 44, 45
— Torymus, 111
Notidobia ciliaris, 42, 43, 45, 57, 58–59
Notonecta, 124

oberthuri, Cataloipus, 67–68
obscurus, Aptinothrips, 90–91
— Tenebrio, 147
obtectus, Acanthoscelides, 150
Odontocerum albicorne, 43, 45
odontogaster, Gerris, 64
Odontothrips cytisi, 91
— meridionalis, 91
— ulicis, 91
Oecetis lacustris, 43, 45, 57–58, 59, 61
Oligotricha ruficrus, 39, 43, 44
olivacea, Phytodecta, 96, 98
Olynx arsames, 103, 107–10
— euedoreschus, 103, 104–6
— gallarum, 103, 107, 111
— — *f.* pulchra, 107, 111
— skianeuros, 103, 110
— trilineata, 103, 106–7
ornatus, Dendrothrips, 90
Oryctes nasicornis, 161
oryzae, Latheticus, 148, 169
— Sitophilus, 144, 148
Oryzaephilus mercator, 148
— surinamensis, 148
ovivorax, Tetrastichus, 103

pagetana, Agrypnia, 39, 43, 44
Palorus ratzeburgi, 147, 148
— subdepressus, 147, 148
paniceum, Stegobium, 144, 151
parabile, Trogoderma, 151
pardalina, Locustana, 79
pellucidus, Glyphotaelius, 43, 44, 45, 58
Perilitus dubius, 96–101
personatum, Sericostoma, 43, 45
Petrobius brevistylis, 81, 84, 86
Phaenobremia aphidivora, 126, 129
philea, Phoebis, 49–56
Phlaeothrips fungi, 92
— ulmi, 92
Phoebis agarithe, 49–56
— eubele, 49, 50
— philea, 49–56
— statira, 49–56
Phryganea cinerea, 45
— grandis, 37, 39, 43, 44, 58, 60
— striata, 43, 44, 58, 60
— varia, 39, 43, 44
physapus, Thrips, 91
Phytodecta olivacea, 96, 98
pilosa, Goëra, 43, 44, 45
Popillia, 159
populi, Tekomyia, 133, 141, 142
postica, Neuronia, 37
Potamophylax latipennis, 43, 45
— stellatus, 42, 43, 45, 58, 61
praetermissus, Thrips, 91
prolixus, Rhodnius, 64
Protoparce quinquemaculata, 160
psalliotae, Henria, 133–42
Pseudeurostus hilleri, 152

psylloides, Gibbium, 152
pteridis, Bryocoris, 64
Ptinus pusillus, 152
— sexpunctatus, 152
f. pulchra, Olynx gallarum, 107, 111
punctata, Corixa, 119–25
pusilloides, Cryptolestes, 148–9
pusillus, Cryptolestes, 148–9
— Ptinus, 152
pygmaea, Heteropeza, 141

quadricollis, Cathartus, 148
quinquemaculata, Protoparce, 160

radiatus, Halesus, 43
ratzeburgi, Palorus, 147, 148
Rhizopertha dominica, 150
rhodesianus, Callosobruchus, 150
Rhodnius prolixus, 64
riparia truncata, Labidura, 23
robusta, Eurytoma, 155–6, 157
robustus, Kakothrips, 92
ruficornis, Atomaria, 159
ruficrus, Oligotricha, 39, 43, 44
rufipes, Necrobia, 150
rufus, Aptinothrips, 90
rutilus, Dinocampus, 96, 97, 98

sabuleti, Ischnodemus, 64
Schistocerca gregaria, 79
schonherri, Anagyrus, 111
Scolopostethus thomsoni, 65
senilis, Athripsodes, 57–58, 61
Sericostoma personatum, 43, 45
serratulae, Eurytoma, 153–4, 155, 156
serricorne, Lasioderma, 144, 150
setiger, Haplothrips, 92
sexpunctatus, Ptinus, 152
Silo nigricornis, 42, 43, 44, 45
Sitophilus granarius, 148
— oryzae, 144, 148
skianeuros, Olynx, 103, 110
Solenotus *sp.*, 103
speyeri, Mycophila, 141
squamosum, Stethomezium, 152
stali, Euborellia, 23, 25
statira, Phoebis, 49–56
Stegobium paniceum, 144, 151
stellatus, Potamophlylax, 42, 43, 45, 58, 61
Stenothrips graminum, 91–92, 93
Stethomezium squamosum, 152
striata, Phryganea, 43, 44, 58, 60
strigifrons, Eurytoma, 156, 157
stylifer, Aptinothrips, 90
subdepressus, Palorus, 147, 148
subfasciatus, Zabrotes, 150
subnubilis, Brachycentrus, 43, 45, 58, 59, 61
subtilissimus, Haplothrips, 92
surinamensis, Oryzaephilus, 148
swynnertoni, Glossina, 9–20, 69–74

tabaci, Thrips, 91
Tabanus thoracinus, 115
Taeniothrips *sp.*, 91
— atratus, 91, 93
— (Rhopalandrothrips) consociatus, 91
— vulgatissimus, 91, 93
talpoides, Hemimerus, 25
Tekomyia populi, 133, 141, 142
Tenebrio molitor, 147, 168, 170
— obscurus, 147
Tenebroides mauritanicus, 151
tenuicornis, Aeolothrips, 89
— Frankliniella, 92
— Humbe, 75–80
Tetrastichus *sp.*, 103
— ovivorax, 103
— xanthomelaenae, 103
thomsoni, Scolopostethus, 65
thoracinus, Tabanus, 115
Thrips *sp.*, 91, 93
— fuscipennis, 91
— imaginis, 94
— hukkineni, 91
— major, 91
— physapus, 91
— praetermissus, 91
— tabaci, 91
THYSANOPTERA, 89–94
tibialis, Eurytoma, 154–5, 156
Tipnus unicolor, 152
tipularius, Neides, 64
Torymus auratus, 111
— cingulatus, 111
— nigricornis, 111
trachypterus, Chrotogonus, 1–4
Trapezonotus *spp.*, 64
Triaenodes bicolor, 43, 61
— conspersa, 37
Tribolium *spp.*, 168, 169
— anaphe, 147
— castaneum, 147, 148, 169, 170
— confusum, 147, 170
— destructor, 147
— madens, 147, 148
Trichogramma cacoeciae, 111
— minutum, 111
Tricholaba barnesi, 126, 129
Trichostegia minor, 39, 43
trifolii, Lestodiplosis, 129
Trigonogenius globulus, 152
trilineata, Olynx, 103, 106–7
Trogoderma anthrenoides, 151
— glabrum, 151
— granarium, 151
— inclusum, 151
— parabile, 151
truncata, Labidura riparia, 23
Tsetse flies, see Glossina
turcicus, Cryptolestes, 148–9, 170, 171

ugandae, Cryptolestes, 148–9
ulicis, Odontothrips, 91
ulmi, Phlaeothrips, 92
unicolor, Tipnus, 152
uniformis, Mansonia, 113
Uranotaenia *sp.*, 113

varia, Phryganea, 39, 43, 44
villosa, Chaetopteryx, 42, 43, 45
vittatus, Limnephilus, 43, 45
vulgatissimus, Taeniothrips, 91, 93

xanthomelaenae, Tetrastichus, 103

Zabrotes subfaciatus, 150

PUBLICATIONS

The principal Publications of the Royal Entomological Society are *Transactions* and *Proceedings.*

The **Transactions** form an annual volume, each paper in the volume being issued as a separate part. The parts are issued irregularly throughout the year.

The **Proceedings** are issued in three series:

Series A.	**General Entomology**
Series B.	**Taxonomy**
Series C.	**Journal of Meetings**

Series A and B are issued in twelve parts, forming an annual volume of approximately 240 pages each.

The following information is supplied for the guidance of authors wishing to submit papers for publication in any of the Society's journals.

TRANSACTIONS

Papers offered for publication in the *Transactions* are considered by the Publication Committee of the Society which meets usually in the months of May and November. In order that papers may be considered at these meetings it is necessary for the manuscript and drawings for illustrations to be in the hands of the Registrar as early as possible. Papers received *after* 1st April and 1st October cannot be considered at the meeting immediately following.

The Society is prepared to undertake the provision of a reasonable number of figures, in line or half-tone. Colour work is accepted only by special arrangement.

Papers of less than eight printed pages (approximately 5,000 words) will not normally be accepted for the *Transactions* and papers by authors who are not Fellows of the Society must be communicated by a Fellow.

PROCEEDINGS SERIES A AND SERIES B

Papers submitted for publication in either *Series A* or *Series B* of the *Proceedings* are considered by the Editor and may be submitted at any time. Papers by authors who are not Fellows of the Society may be accepted if they are communicated by a Fellow.

Line blocks will be provided by the Society. Half-tone and colour work are accepted only by special arrangement and the author may be required to pay for the blocks.

PROCEEDINGS SERIES C

Series C is issued before every General Meeting. It contains abstracts of communications to be made, together with the titles of papers accepted for publication in the *Transactions.*

The annual subscription to *Series A, General Entomology,* is £2 8*s.* 0*d.*; *Series B, Taxonomy,* £2 8*s.* 0*d.*; and *Series C, Journal of Meetings,* £1 0*s.* 0*d.*

As from January, 1936, the journal *Stylops* is continued as *Proceedings Series B, Taxonomy.* Copies of volumes 1–4 are available at £1 16*s.* 0*d.* each, post free.

GENERAL

The original drawings for all figures must be supplied by authors and must be drawn to a scale which will permit of their reduction, singly or after grouping, to an area of dimensions not exceeding 7 by 5 in.

A uniform method is adopted for the citation of bibliographical references in the Society's publications as follows:

SMITH, A., 1935, New species of Coccidae. *Proc. R. ent. Soc. Lond.* (B) 6 : 301–6, pl. 1.

—— 1936, New species of Coccidae. *Trans. R. ent. Soc. Lond.* 84 : 901–36.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals, 3rd edition,* 1952.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

Papers offered for publication should be sent to the Registrar, Royal Entomological Society of London, at 41, *Queen's Gate, London, S.W.*7, and must be typewritten on one side of the paper only, with double spacing. **All papers in the Transactions must be provided with a summary.**

All the Society's publications are copyright.

MEETINGS

TO BE HELD IN THE SOCIETY'S ROOMS
41, Queen's Gate, S.W.7

1962
Wednesday, January 17
„ February 7
„ March 7

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

The Fellowship and Fees

Fellows pay an Admission Fee of £2 2*s*. The Annual Contribution, £3 3*s*., is due on the first day of January in each year, and is payable in advance. Fellows under the age of 25 years on the date of election are exempt from the payment of the Entrance Fee.

Fees should be paid to the Registrar, at 41, Queen's Gate, S.W.7.

Fellows desiring to pay their Annual Contribution through their bankers may obtain an official form of bankers' order by applying to the Registrar.

Fellows whose Contributions for the current year have been paid are entitled to receive the *Transactions* and *Proceedings* of the Society free of charge. Further copies may be purchased at reduced prices by applying to the Registrar.

Forms of application for Fellowship, copies of the Bye-Laws and the List of Fellows may be obtained from the Registrar.

Meetings and Exhibitions

Fellows and others wishing to make a communication to a General Meeting of the Society are requested to send in their names, the title of their exhibit, and a short abstract of their remarks, to the Hon. Secretary fourteen days before the meeting at which it is proposed to make the communication. Should it be desirable to publish a fuller account of the communication the manuscript may be submitted for publication in *Proceedings Series A* or *Series B*.

Fellows resident abroad, or otherwise unable to attend meetings, are reminded that notes or observations sent to the Hon. Secretary may be communicated to a General Meeting on their behalf.

PRINTED FOR THE SOCIETY BY ADLARD AND SON, LTD., BARTHOLOMEW PRESS, DORKING.